

EMBRYOLOGICAL STUDIES
ON
THE FAMILIES BUXACEÆ, MELIACEÆ,
SIMARUBACEÆ AND BURSERACEÆ

BY

JOHAN WIGER

GLEERUPSKA UNIV.-BOKHANDELN, LUND

EMBRYOLOGICAL STUDIES
ON
THE FAMILIES BUXACEÆ, MELIACEÆ,
SIMARUBACEÆ AND BURSERACEÆ

BY

JOHAN WIGER

THESIS

FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, BY DUE PERMISSION OF THE EMINENT
PHILOSOPHICAL FACULTY OF LUND, TO BE PUBLICLY DISCUSSED ON MAY 28 1935,
AT 10 O'CLOCK A. M. IN THE BOTANICAL LECTURER HALL.

LUND
PRINTED BY HÅKAN OHLSSON
1935



Digitized by the Internet Archive
in 2026



EMBRYOLOGICAL STUDIES
ON
THE FAMILIES BUXACEÆ, MELIACEÆ,
SIMARUBACEÆ AND BURSERACEÆ

BY

JOHAN WIGER

LUND
PRINTED BY HÅKAN OHLSSON
1935

*34073



Preface.

The Order of Terebinthales (system of WETTSTEIN) has been hitherto insufficiently known with regard to its embryological development. Certain families are quite unknown. Of the larger ones only *Rutaceae* has been a little studied, of some others one or two species have been more or less examined. The present study aims at spreading some light upon the development of ovules and pollen in some families of this Order. As to *Burseraceae* no information is to be found in the literature. Of the nearly related families *Meliaceae* and *Simarubaceae* there are some notices published on one or two species of each. Of the small family *Buxaceae*, in the system of ENGLER and PRANTL associated with the families mentioned above, by WETTSTEIN, however, placed in the Order of *Tricoccae*, there are some statements given about two genera, *Buxus* and *Sarcococca*.

With the exception of mature seeds of *Pachysandra terminalis* and *Alvaradoa amorphoides* which have been macerated in the usual manner of herbarium material, only fresh fixed material was used for the present investigation. Considerable difficulty has been experienced in procuring working material. With the exception of the family *Buxaceae* and some species of *Meliaceae* and *Simarubaceae* the whole material consists of tropical plants. *Burseraceae* has no representatives outside the Tropics. Moreover, as these plants for the most part are big trees, in many cases imposing members of the tropical forests, it may be conceived that little material for embryological studies will be found in our plant-houses. Fully aware of the difficulties of such an undertaking I however made an attempt to get the assistance of tropical botanists for the collecting work. An extensive correspondence requiring much time took place, as is evident from the following list of my collectors and helpers. It would have cost too much time and money to collect myself the material received. I am therefore greatly obliged to the gentlemen in the Tropics and elsewhere for their kind help in this matter. In spite of the difficulties mentioned above I can say, however, that the characteristic traits of the development of the families studied have been elucidated.

Most of the material was sent to me from the Botanic Garden at Buitenzorg, Java. For this ready and valuable help I express my thanks to the following gentlemen: Dr. K. V. DAMMERMANN, Director of the Garden; Dr. F. W. WENT, Head of Treub Laboratory, and Dr. H. J. LAM, later on Head of the same Laboratory; Dr. T. Å. TENGWALL, Buitenzorg. A later collection from the same Garden was

fixed by Fil. Lic. IVAR ELVERS, Stockholm, for which unselfish help I thank him heartily.

For further collections I am indebted to the following botanists in different parts of the world: Dr. F. SHREVE, Head of the Desert Laboratory of the Carnegie Institution of Washington, Tucson, Arizona; Mr. T. D. MALLERY, member of the staff of the same Laboratory; Mr. J. S. DASH, Director of the Department of Agriculture, Georgetown, Brit. Guiana; Dr. R. S. HOLTTUM, Director of the Botanic Gardens, Singapore; Mr. N. D. SIMPSON, Systematic Botanist, Dep. of Agriculture, Peradeniya, Ceylon; Mr. H. PERRIER DE LA BATHIE, Majunga, Madagascar; Sir ARTHUR W. HILL, Director of the Royal Botanic Gardens, Kew, London; Dr. C. R. METCALF, and several members of the staff in the same Garden (who assisted me in the fixing work during my visit to this Garden in 1932); Mr. M. Y. ORR, Royal Botanic Garden, Edinburgh; C. CONZATTI, Professor of Botany, Oaxaca, Mexico. I thank further: Mr. A. LANGE, Curator, Botanic Garden, Copenhagen, who has kindly given me much time during my numerous visits to this Garden; Dr. ERIK ASPLUND, Riksmuseum, Stockholm, who has assisted me in several ways; Fil. Kand. TH. ARVIDSSON, Stockholm (for fixing and determination of a *Buxus* species); T. NATHORST-WINDAHL, Director, and C. BLOM, Amanuensis, Botanic Garden, Gothenburg (Mr. BLOM has also determined several *Buxus* species); Dr. A. FRISENDAHL, Lecturer, Gothenburg.

For addresses and recommendations Professor Dr. H. M. HALL, Stanford University, Berkeley, Calif.; Dr. vet. HENRY POISSON, Tananarive, Madagascar; Professor Dr. O. ROSENBERG, Stockholm; and Dr. G. TURESSON, Academical Docent, Lund, were helpful.

At the publishing of this work I thank the late Professor Dr. TH. C. E. FRIES, Lund, for much good advice and help during my studies; further Dr. A. HÅKANSSON, Academical Docent, Lund, and Professor Dr. H. KYLIN, Lund, who later on in various ways had to do with my work and studies. Dr. J. MAURITZON, Academical Docent, Lund, has collected some material for me and further given me good advice in connection with the printing of the present specimen, for which I express to him my thanks.

In the summer of 1932 I received from the Kungl. Fysiografiska Sällskapet in Lund an exhibition (200 kr.) as a contribution towards the cost of the material. For this help I herewith express my thanks.

Finally, I thank Mr. C. ALLWOOD, Jönköping, and Dr. A. ÅKERLUND, Lecturer, Halmstad, for their kind help with the English translation and proofreading of this paper.

For the fixing was used, for the most part, the solution recommended by KARPETSCHENKO, which gave good results. Other fluids, e. g. those of JUEL, CARNOY or ZENKER, have also been used in some cases. The staining was done with HEIDENHAIN's iron-alum-hæmatoxylin, and light green. The thickness of the sections varied between 5 and 15 microns.

Halmstad, April, 1935.

Buxaceae.

The family of the *Buxaceae*, according to PAX (1896), and other authors, comprises six genera, with about 30 species. Of these I have examined 12 species out of four genera, namely: *Buxus sempervirens* L., *B. balearica* WILLD., *B. microphylla* S. & Z. var. *japonica* REHD. & WILS. (below called only *microphylla*), *B. Wallichiana* BAILL., *Sarcococca pruniformis* LINDL., *S. Hookeriana* BAILL., *S. humilis* STAFF., *S. Zeylanica* BAILL., *S. ruscifolia* STAFF., *Pachysandra procumbens* MICHX., *P. terminalis* S. & Z., and *Simmondsia californica* NUTT.

Buxus, *Sarcococca* (with the exception of *zeylanica*), and *Pachysandra* were collected in the Botanic Gardens of Lund, Gothenburg, Stockholm, Copenhagen, Edinburgh, and London. *Sarcococca zeylanica* and *Simmondsia* are from wild specimens in Ceylon and Arizona, respectively.

Two monographs have been published on this family, viz., one by BAILLON (1859) and another by VAN TIEGHEM (1897). The former lays stress upon the autonomy of the *Buxaceae*, as opposed to the *Euphorbiaceae*, these two families having formerly been associated, more or less, by several authors, e. g. BENTHAM and HOOKER (1883). VAN TIEGHEM published later on another paper on the *Buxaceae*, in which he made some new classifications of them. Thus he singled out the *Simmondsia*, this genus in many respects differing from the rest of the *Buxaceae*, and constituted it as a special family, giving it the name of *Simmondsiaceae*. He held the opinion that this family was more akin to the apetalous Centrosperms.

Some short embryological notices exist concerning this family. Thus, JÖNSSON (1880) in a few words states correctly that the embryo sac in *Buxus sempervirens* develops according to what is nowadays called normal type, although his interpretation of the tetrad is not quite correct, when he speaks of »three daughter cells». The endosperm of this species was elucidated by SAMUELSSON (1913) who found it to be ab initio cellular. ORR (1923) found polyembryony in *Sarcococca ruscifolia*, and I myself proved, some years later (1930), that the polyembryony which occurs also in *S. pruniformis* originates in nucellus, and that in this species there is formed an embryo sac of normal type, which, however, degenerates, with the exception of the polar nuclei, these giving rise to a nuclear endosperm. As no pollination occurs I arrived at the conclusion that this nucellar embryony must be regarded as quite autonomous. DAHLGREN has a phenological statement on the

pollen and the embryo sac in *Buxus sempervirens* (1915), and the »fausses cloisons» in the ovary of the *Pachysandra* were pointed out as early as 1871 by VAN TIEGHEM, and afterwards by CELAKOWSKY (1893), but this seems to have escaped the systematists (BENTHAM and HOOKER, 1883, PAX, 1896, p. 131).

Gynaeceum. Placentation.

The flowers of the family are carefully described in the above-mentioned monographs and in the systematic manuals (EICHLER 1878, PAX 1896, a. o.). As there is a certain lack of accord in older systematical statements about the position of the carpels in relation to the sepals in *Buxus*, I shall here say a few words on this matter. The species studied are all monoecious, except *Simmondsia*, which is dioecious. In the case of the former, the sexes are placed in the same inflorescence, in these *Buxus* species a headlike one. Fig. 1 A and B show length- and cross-sections through the inflorescence in *Buxus sempervirens*. A female flower occurs terminally, and below this are the male flowers. BAILLON (l. c., p. 25) and MÜLLER (DE CANDOLLE, Prodrum, XVI, 1, p. 14) state that the carpels alternate with the nearest placed sepals. EICHLER (Blüthendiagr. II, p. 401), on the other hand, says that they are superposed, which is also seen from his fig. 163 (reproduced by PAX 1896), adding, however, in a footnote that he is not altogether confident that this view of his is correct. From my fig. 1 B it appears that the older systematists are indeed in the right, and that EICHLER (and, accordingly, PAX with him) are wrong. Alternation is the case throughout in *Buxus sempervirens*.

Buxus balearica shows a tendency towards developing bisexual flowers nearest to the terminal female flower. These bisexual flowers have more or less abnormal, partly open ovaries. Fig. 1 C shows a section of such a flower, with two carpels of female character and the third of male character. The first two had three rather normal ovules and a fourth ovule with orthotropic position and imperfect integuments. All of them had an embryo sac. The male carpel had, level with the ovules, some pollen sacs in the shape of irregular protuberances, containing darkly coloured tissue rests, or some normal pollen mother cells. Also on the insides of the styles there were more or less abnormal pollen sacs, with pollen. Sometimes the terminal flower, too, of this species shows similar bisexual tendencies, with pollen sacs on the styles, etc.

The development of the ovary shows certain differences between, on one hand, *Buxus*, *Sarcococca*, and *Pachysandra*, which resemble each other, and, on the other hand, *Simmondsia*. The earliest stage is described by BAILLON (1859), as regards the first group. The ovary is, in the beginning, a small bowl-shaped papilla, formed by two or three carpels. In the sutures between these arise the placentas (marginal placenta), and there are two ovules, each belonging to its carpel. Fig. 1 D shows transverse section of the organ at this time in *Sarcococca pruniformis*.

BAILLON points out that the placentation at this stage of development is in fact parietal (cf. VAN TIEGHEM, 1897, p. 289). When soon the placentas grow together in the centre, the ovary gets divided into three cells, each containing two pendent apical ovules belonging to one and the same carpel (central placenta). At the same time the carpels grow out into styles.



Fig. 1. A-B, K-L *Buxus sempervirens*. A Longitudinal section of young inflorescence. $\times 50$. B Transverse section. $\times 50$. K Transverse section through styles and nectaries (n). $\times 12$. L Longitudinal section through gynaeceum. $\times 9$. C *Buxus balearica*. Longitudinal section through bisexual flower. $\times 5$. M *Buxus Wallichiana*. E. M. C. $\times 300$. D-I *Sarcococca prunifolia*. D Transverse section of young ovary, ov ovule, pl placenta. $\times 50$. E-H Transverse sections of gynaeceum: E through upper part of style, F through upper, G through middle, and H through lower part of ovary. $\times 50$. I Longitudinal section through gynaeceum. $\times 50$.

Fig. 1 E-L, 2 L-O show transverse and longitudinal sections through the gynaeceum in the three genera *Buxus*, *Sarcococca*, and *Pachysandra*. The following points may be noticed: the styles are free, in *Buxus* somewhat short and thick and at the points more or less broadened out into stigmas; in *Sarcococca*, and *Pachysandra* a little longer, bent or rolled backwards. They do not fall off, but remain on the fruit, in the shape of small tips. The styles have ventral furrows, leading down into the ovary cells. A palisade-like epidermis covers the insides

of the styles and the ventral furrows. *Pachysandra* has frequently only two carpels and differs from the others in that the cells, by means of median laminae («fausses cloisons», VAN TIEGHEM, l. c.) on the insides of the carpels, are divided into two parts, so that they become uniovular (fig. 2 N-O). These «fausses cloisons» are considerably thinner than the other walls, as appears from the figures. In *Pachysandra terminalis* there has been observed a peculiar growth of abnormal ovules in the ovary, about which more below.

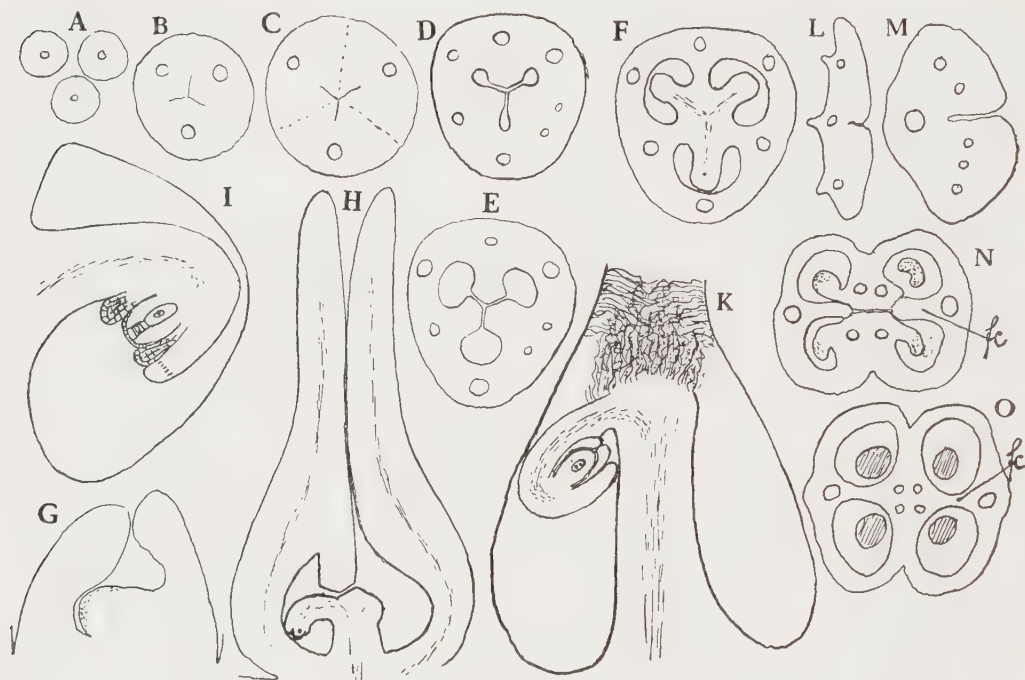


Fig. 2. A-K *Simmondsia californica*. A-F Transverse sections of gynaecium. $\times 35$. A through styles. B-F through different levels of ovary. G-K Longitudinal sections: G through young gynaecium. $\times 80$. H-K showing different positions of ovule H, K $\times 35$, I $\times 80$. L-O *Pachysandra procumbens*. Transverse sections through: L upper, M lower part of style, N upper, O lower part of ovary, fc «fausses cloisons». $\times 15$.

In *Buxus* we have interstylar nectaries in the shape of small protuberances (see fig. 1 K, L), composed of a plasma-filled parenchyma, «riche en sucre et recouvert d'un épiderme qui offre, rapprochés vers le sommet, un petit nombre de stomates aquifères, ordinairement de deux à huit» (VAN TIEGHEM, 1897, p. 308).

The vascular strand leading into the ovary, often divided into several smaller ones, goes up through the placenta and sends branches to the ovules. Each of the carpels receives one larger median strand and a number of smaller lateral strands.

In *Simmondsia* the gynaecium presents some diverging features, which I shall touch upon, referring to fig. 2 A-K.

From the transverse sections in fig. 2 A-F, it appears that the carpels in *Simmondsia*, as in the other genera, are three. The styles, free and cylindric, fall off. They are devoid of ventral furrows and have an axial vascular strand. Stigmas are missing. A palisade-like epidermis, later on elongated into a short pilosity, covers the styles. In the upper part of the ovary appear ventral furrows on the carpels (fig. C), going down into the ovary cells.

The placentation differs somewhat in this genus, as shown by the longitudinal sections, fig. 2 G-K. Fig. G gives a section through a young gynaeceum, showing a basal ovular papilla, and above this the carpels leaning together and forming an ovary. In fig. H is seen how the placenta, formed by the turned-in basal parts of the carpels, rises from the bottom of the ovary in the shape of a three-winged column, bearing the ovules in a horizontal position. Above this pillar the ovary partitions communicate. The carpels elongate into styles. In the course of development, the placenta, with the ovules, gradually reaches the upper parts of the chambers. Fig. 2 I-K show later stages, with the apotropous curve. In the upper part of the ovary the ovules ultimately obtain a pendulous position. Only one carpel edge is fertile in *Simmondsia*, this species thus having a single ovule in each partition (fig. 2 F).

This peculiar placentation is mentioned by earlier authors. MÜLLER says (1869, p. 32): »ovula ex parte superiore non ex apice loculorum pendula». VAN TIEGHEM describes it, in detail, in the following manner, evidently having in mind a stage corresponding to fig. 2 I: the ovule is »attaché vers le milieu de l'angle interne de chaque loge. Cette insertion de l'ovule à mi-hauteur tient à une conformation particulière de l'ovaire. Les carpelles, en effet, ne sont unis au centre que jusqu'au-dessus de l'insertion des ovules; au delà, ils deviennent libres suivant l'axe, quoique encore appliqués l'un contre l'autre, et laissant entre eux un étroit canal communiquant avec chaque loge par une petite fente au-dessus de chaque ovule». The epidermis of the placenta, and of the narrow slits above, is, in the course of the development of the embryo sac, lengthened into a long pilosity (fig. 2 K). A rather thick vascular bundle goes up through the placenta, sending out a branch to each of the ovules. In the wall of the ovary there are three larger and a number of smaller vascular strands. In *Simmondsia* there are no interstylar nectary protuberances.

Archegonium. Integuments.

As has been mentioned above, the ovule in *Buxus*, *Sarcococca*, and *Pachysandra* is ab initio an apical, pendulous papilla. It is then composed of a homogeneous parenchyma with an epidermis. At a very early stage, the apotropous curve is commenced, by a stronger growth at one side of the funiculus. The archesporial cell is now being formed, hypodermally; conspicuous through a denser plasma, a larger nucleus, and likewise a larger nucleolus (fig. 3 A, 4 B, C). Sometimes

several hypodermal archesporial cells have been found, but it is only in exceptional cases that more than one attains a further development (fig. 3 D); and only one divides heterotypically.

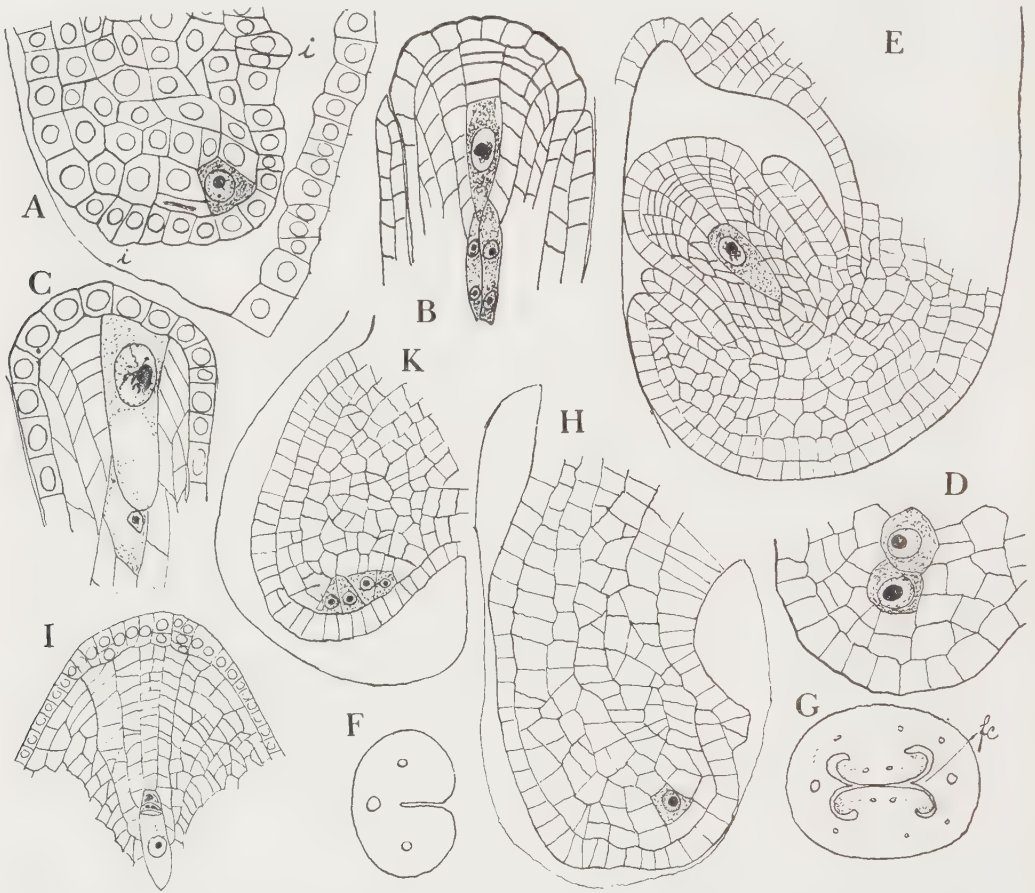


Fig. 3. A-C *Sarcococca pruniformis*. A Subepidermal archesporial cell, commencement of integument (*i*). $\times 365$. B E. M. C. and nutritive cells in chalaza. $\times 300$. C Subepidermal E. M. C. $\times 365$. D *S. Hookeriana*. Two E. M. C. $\times 600$. E *Pachysandra procumbens*. E. M. C. Commencement of obturator. $\times 180$. F-H *Pachysandra terminalis*. F-G Transverse section through style and ovary, *fc* «fausses cloisons». F $\times 20$. G $\times 10$. H Archesporial cell under one parietal cell. $\times 300$. I *Buxus microphylla*. Triad under 13 parietal strata, nucellus-cap. $\times 180$. K *Simmondsia californica*. Several archesporial cells, commencement of integument. $\times 300$.

The many-celled archesporium has been discussed by several authors. Not intending to go into details on this point, I only refer to SCHNARF (1927—29, 69 a. f.).

The inner integument is formed at the same time as the archesporium in a circular zone beneath the nucellus-point, in the following manner: two epidermis cells elongate in a radial direction and divide periclinally (see fig. 3 A, 4 B).

Thus, in the genera now mentioned, the double layer in this integument is, *ab initio*, visible. In e. g. *Buxus balearica* there is, later on, frequently to be seen a thin intermediate layer in the upper part of the inner integument.

Simmondsia differs a little from the genera mentioned above. Before the ovular papilla has risen from its basal position, the apotropous curve commences. The ovule is then not yet differentiated, but soon the archesporial cell and the inner integument are formed in the same way as in the above-mentioned genera, with the difference that in *Simmondsia* this integument is many-layered (fig. 4 F). Here, too, several cells in the nucellus point have sporadically presented an archesporial character (fig. 3 K).

The archesporial cell, in all species, gives rise to a parietal or tapetal cell, which later on divides periclinally as well as anticlinally, the archesporial cell thus being moved into the nucellus. These plants, accordingly, have an ovule of the crassinucellate type, as was noticed by JÖNSSON in *Buxus sempervirens*. Especially this last-mentioned genus develops a very massive nucellus (fig. 3 I).

The outer integument is formed in a horse-shoe-shaped zone below the point of the inner, and is many-layered. It is lacking on the raphe-side.

While proceeding into the nucellus, the archesporial cell grows, and assumes, in all the species investigated, the traits that are characteristic of the heterotypical prophase. Synapsis, especially, has often been observed. Thus, in these plants, the E. M. C. (=embryo sac mother cell) is no doubt subjected to reduction division. The number of parietal cells is not quite the same in the different species. In *Simmondsia*, which has a weak nucellus, I have observed dyads under but two parietal cells (fig. 5 T), but as a rule, there are five (fig. 4 G). In *Sarcococca* the tetrad division occurs under 4—6 parietal cells, which later on increase to about 8. The *Pachysandra* species form 7—10 parietal cells, whereas *Buxus* develops no less than 10—15, or more. Only in *Buxus balearica* have I, exceptionally, observed heterotypical division with as few as 4 parietal cells. In *Buxus sempervirens* I observed a certain degree of variation in this respect, possibly due to the fact that several somewhat different forms, existed in my material. This will clearly appear from a comparison between my fig. 4 D and E. In fig. D the parietal cells are five, the heterotypical division is already begun, and the apotropous curve of the ovule is not yet finished. In the ovule of fig. E the parietal cells were about twelve, the division of the E. M. C. was not commenced, and the apotropism had been accomplished. The integuments are also more developed in this ovule. JÖNSSON says that the parietal cells may amount to 7—11, which statement, therefore, does not hold good in all cases.

Fig. 2—4, 5, 7 show E. M. C., nucellus, and integuments in a number of species. The inner integument grows more rapidly in *Buxus* than in the other genera, as is seen from the figures. In *Buxus* the micropylar canal closes already before or in the course of the tetrad division, in other species not until the completion of the E. S. (=embryo sac). In these plants no integument tapetum is formed. It is true that the integument cells elongate, more or less in earlier

stages, but later on a flattening of the cells ensues. Only around the micropylar canal do they sometimes retain this shape. JÖNSSON (l. c.) states erroneously that in *Buxus sempervirens* the inner integument thickens at the point. This is, however, the case in *Simmondsia* (fig. 7 I). Periclinal division in the epidermis of the nucellus point has been observed in *Buxus*, *Simmondsia*, and *Pachysandra terminalis* (fig. 3 I, 4 A, G, a. o.) but is restricted to about four cell layers; wherefore

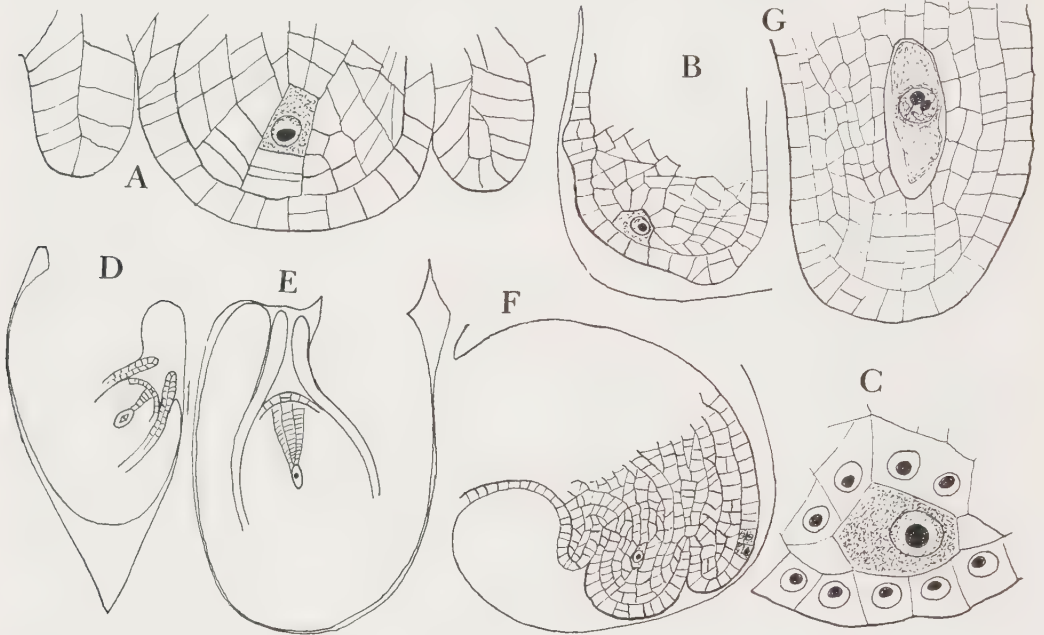


Fig. 4. A *Buxus balearica*. E. M. C. under 3 parietal cells. $\times 485$. B-E *Buxus sempervirens*. B Archesporial cell. $\times 300$. C Same. $\times 900$. D E. M. C. in process of division under 5 parietal cells. E Ditto, not yet divided, under 12 strata of cells. See text. $\times 70$. F-G *Simmondsia*. F Inner integument, many-layered. Outer integument commenced. $\times 180$. G E. M. C., 5 parietal cells. $\times 485$.

I cannot agree with JÖNSSON (l. c.), when he speaks of »a strong cap-formation» in *Buxus sempervirens*. Nor can one, as he says, distinguish any sharp line of demarcation between the original nucellus and the cap. The *Sarcococca* species and *Pachysandra procumbens* have no periclinal division in the nucellus epidermis. In some cases I have observed, in *Sarcococca pruniformis*, that a hypodermal cell has developed directly into an E. M. C. (fig. 3 C).

Under the E. M. C. lie, in *Sarcococca* and *Pachysandra*, a bundle of rather long, plasma-filled, often two-nuclear cells, which have no doubt an important task as nutrition conductors (fig. 3 B). Similar cell bundles have been mentioned by e. g. PALM for *Dahlia coronata* (1915, p. 197), and by STENAR for *Phacelia tanacetifolia* (1925, p. 18), and others. Later on they become empty and get refractive walls. In the chalaza *Sarcococca* and *Pachysandra* also develop a hypostasis of small cells, with, later on, thickened and refractive walls.

The tetrad division.

When just before the tetrad division the E. M. C. is at the height of its development, it frequently attains considerable proportions, as in *Sarcococca pruniiformis* and *Pachysandra procumbens*. The cell in fig. 3 B was found to be about 60 μ in length. The nuclei are, likewise, of remarkable size (20 μ in length). These have, as the figures show, in cylindric cells a pronounced oval form. In *Buxus* they seem to be spherical also in lengthened cells. On the relations between the shape of the cell and that of the nucleus we have a statement by TISCHLER (1921, 4 a. f.), who considers that a connection exists, but whether active or passive on the part of the nucleus, has not yet been made clear.

After the stages of synapsis and of spirem which have been observed in all the species, the chromosome formation commences in the E. M. C., whereupon development proceeds more rapidly. Diakinesis has been observed in some species, e. g., in *Sarcococca pruniiformis*. The number of chromosomes is here difficult to establish, as a certain irregularity seems to prevail and the chromosomes are small and numerous. The haploid number might, however, be about 30. Heterotypical division stages have been observed in several species, for instance in *Sarcococca pruniiformis*, *Buxus sempervirens*, *B. balearica*, *Pachysandra procumbens*, and *terminalis* (fig. 5 A, F, N, S.). In all these cases the spindle has always been found somewhat above the middle of the cell, which may be worth pointing out, as a contribution to the discussion about the frequently observed dissimilarity in the size of the macrospore cells. As is commonly known, these increase in size towards the chalaza, but how this is done, if they are originally of uniform size and the chalaza cells afterwards, by means of a secondary growth, become larger; or, if they are from the very start unequal, on this point there is not a little uncertainty, and, upon the whole, only a few observations have been made. »Diejenigen Fälle, wo ein Autor bewusst diese beiden Ursachen unterschieden hat, sind ziemlich vereinzelt.» (SCHNARF 1929, p. 104.) Distinct statements on this matter are made by, e. g., PALM (1915) as regards *Dahlia coronata*, and by JUEL (1900, p. 17) concerning *Antennaria dioica*. Both authors ascribe the dissimilarity to the position of the spindle, and in this I can agree with them, as far as the species here mentioned are concerned. Fig. 5 F shows a heterotypical anaphase in *Buxus sempervirens*. The beautifully undulating wall in the spindle had evidently not yet got attached to the mother cell wall when the fixing fluid penetrated and contracted the cytoplasm. The heterogeneous chromatin bodies probably represent chromosome fusions, as, in other cases, I found that this species has very small chromosomes. Fig. 5 N is a heterotypical metaphase in two sections from *Buxus balearica*, in which the rather large haploid chromosomes can be counted to 8. Fig. 5 R stands for *Pachysandra procumbens*. Both in a metaphase and in this interkinesis I think that I can fix the number of the haploid chromosomes to about 10 or 11. Fig. 5 S shows a fine nuclear spindle,

metaphase or commencing anaphase, in *Pachysandra terminalis*. The spindle threads were distinctly separate, fairly thick, and running out into pointed poles, in the way the figure shows. The chromosomes sat in the shape of small bodies

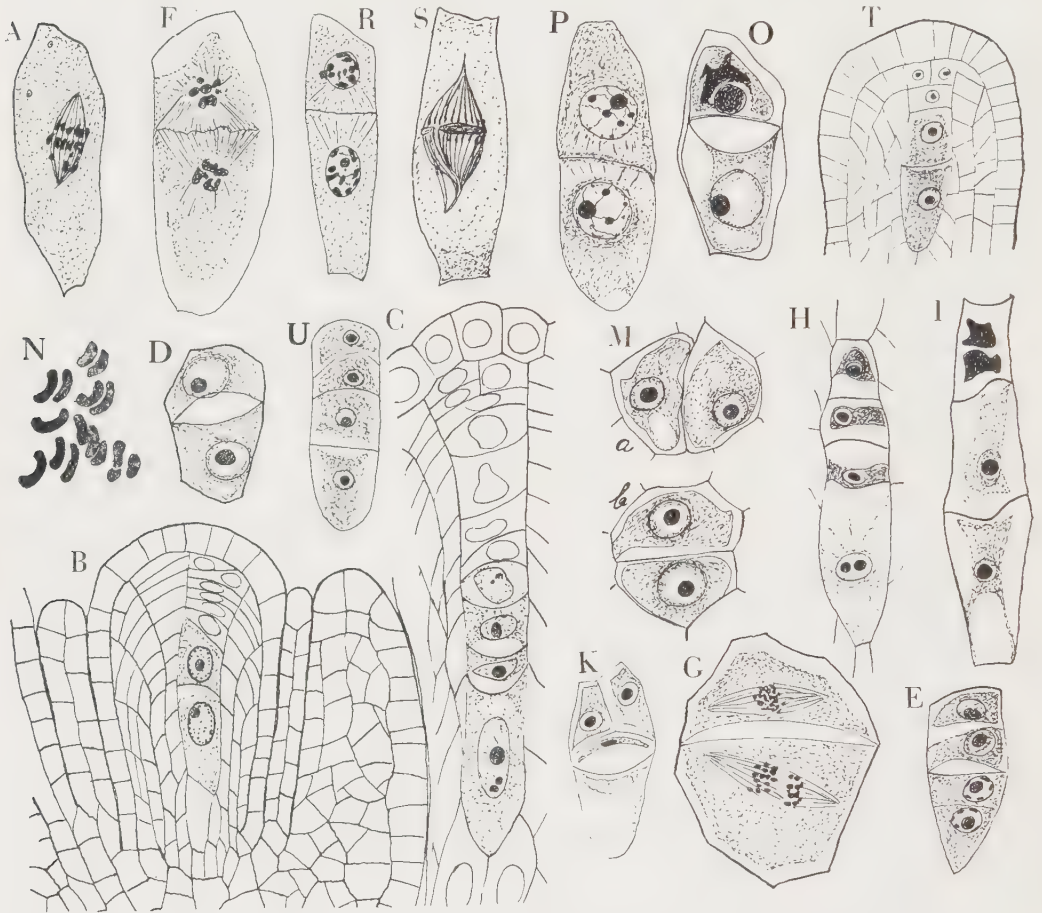


Fig. 5. *A-C Sarcococca pruniformis*. *A* Heterotypic division. $\times 365$. *B* Dyad. Integument. $\times 365$. *C* Tetrad. $\times 600$. *D-E Sarcococca humilis*. *D* Dyad. $\times 900$. *E* Tetrad. $\times 485$. *F-M Buxus sempervirens*. *F* Heterotypic anaphase. $\times 830$. *G* Homotypic division. $\times 1030$. *H-I* Tetrads. $\times 600$. *K* T-tetrad. $\times 600$. *M a-b* Tetrahedral tetrad. Two consecutive sections. $\times 1030$. *N-O Buxus balearica*. *N* Heterotypic metaphase. 8 gemini. $\times 1800$. *O* Upper dyad cell in course of degeneration. $\times 830$. *P Buxus microphylla*. Dyad. $\times 600$. *R Pachysandra procumbens*. Interkinesis, about 10–11 chromosomes. $\times 600$. *S Pachysandra terminalis*. Heterotypic spindle. $\times 1030$. *T-U Simmondsia californica*. Dyad. $\times 485$. Tetrad. $\times 600$.

on the spindle threads on either side of the thick, yellow-coloured cell plate, which did not reach beyond the spindle and seemed to be uncompleted. Finally, fig. 5 *A* shows a heterotypical division figure in *Sarcococca pruniformis*. A certain degree of irregularity seems to exist in the wanderings of the chromosomes towards the poles.

The heterotypical division is accompanied by a wall formation, so that two dyad cells arise. Such have been observed in the following 8 species: *Buxus sempervirens*, *balearica*, *microphylla*, *Sarcococca pruniformis* and *humilis*, *Pachysandra terminalis* and *procumbens*, and *Simmondsia californica*. In all cases the nether chalazal cell has been larger than, or as large as, the upper, as in *Buxus microphylla* (fig. 5 P). The figures 5 B, D, O, P, R, T show dyads in different species. The walls between the cells have often been thickened into strongly convex lenses (see figures). The dyad nuclei then divide and give, as a rule, rise to normal row tetrads. Such tetrads have been observed in *Buxus sempervirens*, *Sarcococca pruniformis*, *ruscifolia*, *humilis*, and *Hookeriana*, the *Pachysandra* species, and *Simmondsia* (fig. 5 C, E, H-I, U, 6 L, N).

A T-formed disposition has been seen in *Buxus sempervirens* (fig. 5 K) and *Sarcococca pruniformis* (fig. 6 A). In the latter case the E. M. C. had been subepidermal, which has, by the bye, been observed several times in this species. Other dispositions of the tetrad cells have also been observed. Fig. 5 G shows dyad spindles in *Buxus sempervirens*, both lying transverse as well as parallel, wherefore a location of the megaspores would here have resulted in what SCHNARF (1929, p. 98) terms quadratic, »d. h. zwei übereinanderliegende Paare nebeneinanderliegender Makrosporen, durch parallele Lage der beiden quergestellten homöotypischen Spindeln entstanden». The author in question states that this disposition of the tetrad cells seems to be extremely rare. In *Aristolochia Clematidis*, which, according to JACOBSSON-STIASNY (1918) has, for the most part, only abnormal tetrads, quadratic and T-formed disposition appeared equally often, whereas row tetrads were exceptional. Another plant with quadratic tetrad is *Pittosporum Timorense* (BREMER 1916). The above-mentioned case in *Buxus sempervirens* is the only one observed. As appears from the figure, there is, practically synchronism between the two dyad spindles, the inner being only a trifle more advanced. As usual, this cell is also somewhat larger. The chromosomes are small and numerous, their number being, approximately, 15—20 in the inner spindle.

In *Buxus sempervirens* a tetrahedral disposition of the cells has also, in several cases, been observed, as shown by fig. 5 M. As we have here to do with two consecutive sections in longitudinal direction, the heterotypic spindle has, thus, been transverse, and as for the two homotypic ones, the one has had length- and the other cross-position. I have not been able to find any such case mentioned in the literature of the subject, whereas SCHNARF (1929, p. 99) gives some instances of tetrahedral tetrads with both the homotypic spindles placed transversely and crosswise.

Other deviating megaspore positions have been found in this species. Fig. 6 C shows a peculiar tetrad, consisting of four cells in the same vertical plane, two outer and two inner, which are larger. One of the latter presents a division figure; one of the former was evidently in a process of degeneration, with contracted and strongly tinged cytoplasm. Which two of these four are sister

cells, may perhaps be left open to discussion. For my part, I am inclined to the belief that the homotypic spindles have lain parallel, lengthwise. The tetrad, I take it, might be regarded as a quadratic one, although with another disposition of the dyads than in the above-mentioned quadrate tetrad. Most probably the

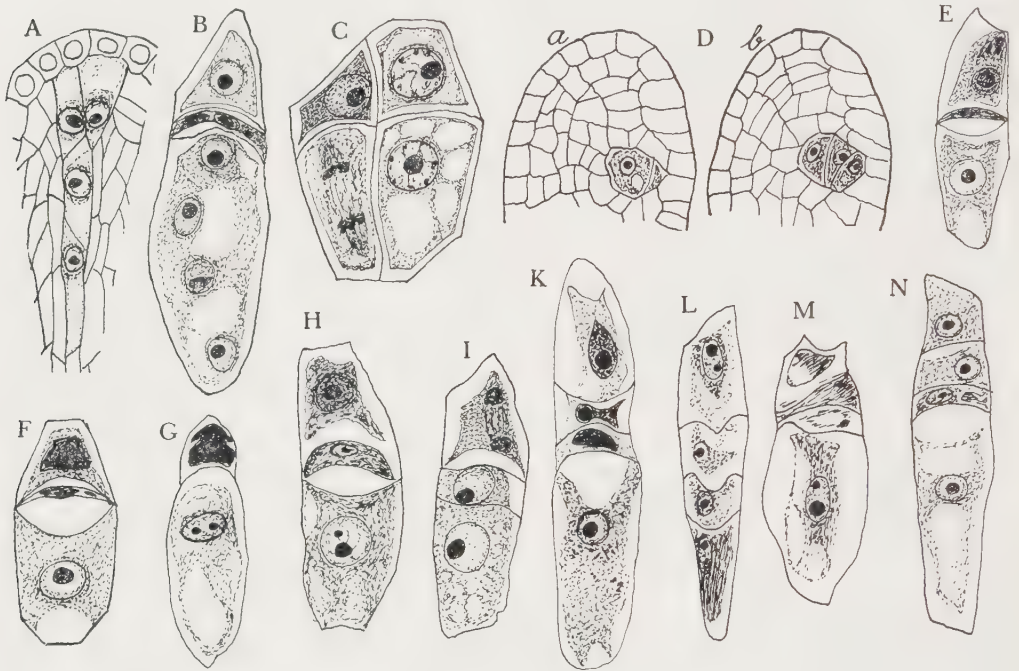


Fig. 6. *A Sarcococca pruniformis*. T-tetrad. No parietal cells. $\times 340$. *B Sarcococca humilis*. 4-nucleate E. S. Upper triad cell vital. $\times 600$. *C-E Buxus sempervirens*. *C* Quadratic tetrad, see text. $\times 830$. *D a-b* Acentric quadratic tetrad in two consecutive sections. $\times 300$. *E* Upper dyad cell, undivided, degenerating. $\times 600$. *F-G Buxus balearica*. *F* Triad. Upper dyad cell degenerating. $\times 600$. *G* 1-nucleate E. S. $\times 600$. *H-I Buxus microphylla*. *H* Triad, see *F*. $\times 600$. *I* Upper dyad nucleus divided, no cell wall. $\times 600$. *K Simmondsia californica*. Tetrad with chalazal cell developed into 1-nucleate E. S., also micropylar megaspore advanced. $\times 600$. *L-M Pachysandra procumbens*. *L* Tetrad with micropylar megaspore most advanced. $\times 600$. *M* 1-nucleate E. S. $\times 600$. *N Pachysandra terminalis*. Tetrad with 1-nucleate E. S. $\times 600$.

inner left hand cell had the start, from the beginning, and began playing the rôle of an E. S. by proceeding to nuclear division, but later on its right hand neighbour seems to have commenced outgrowing it. It would seem evident that there exists a tendency towards further development in the inner pair of cells, in this type of tetrad, and at the same time a certain antagonism between the two. Other authors have also called attention to this. CARANO (1915) saw, in *Poinsettia pulcherrima*, that in quadratic and tetrahedral tetrads two, or three, or all the four cells tended towards further development. JACOBSSON-STIASNY (1918) observed in *Aristolochia Clematitis* that, in linear tetrads, the chalazal megaspore

dominated, but that, where the cell disposition was a more agglomerated one, there were several showing tendencies of development.

There is, in *Buxus sempervirens*, one more abnormal location of the megaspores to be mentioned, fig. 6 D. We first remark the acentric position of the tetrad in the nucellus, and the palisade-like shape of the epidermal cells at the nearest side. The tetrad consisted of one larger and three smaller cells in about the same horizontal plane, but not in a row, and thus we may perhaps be justified in declaring this position to be a quadratic one, with, however, yet another placing of the spindles than in the two above-mentioned cases. Here, heterotypic as well as homotypic spindles have evidently lain transversely, and in the same plane. The large cell may have constituted the E. S. Thus, we have seen that in *Buxus sempervirens* there exist both linear, T-formed, and tetrahedral tetrads, and further three different types of quadratic tetrads. The last four were found in the same gynaeceum. I have cut a large material of this species, and it is quite probable that deviations would be found in other plants as well, if only the material investigated were sufficiently extensive. TISCHLER (1921, p. 369 a. f.) considers that the shape of the E. M. C. predisposes to a linear or a tetrahedral placing of the megaspores: if the E. M. C. is a lengthened one, we get the former alternative, if it is rounded, the latter.

In all the above cases of deviations from normal tetrad division, the result has been four cells. In some species the upper dyad cell degenerates, so that triads, so called, arise. Instances of this are to be seen in some of the figures given. Fig. 5 O is a dyad of *Buxus balearica*, in which the upper cell shows a clear tendency towards degeneration. The plasma was strongly tinged, and the nucleus contracted to a black, round body. The cell walls were thickened, and especially the wall between the cells was swollen into a strongly convex, green-coloured lens. Fig. 6 F gives a triad in the same species. The upper dyad cell degenerates undivided, the lower has detached a smaller sister cell, also degenerating. In this case, too, the latest-formed wall consisted of a strongly swollen, green lens. Fig. 6 G represents a primary E. S. with a black-coloured remnant of two upper cells. I have seen no normal tetrad in this species, but only such triads as have been described above, wherefore this may be supposed to be the rule.

Buxus microphylla presents similar deviations. Fig. 5 P shows a normal dyad, fig. 6 H, on the other hand, the same state of things as in *balearica*, viz., a triad consisting of one vigorous chalazal cell and two degenerating upper ones, which no doubt represent the sister cell of the lower and the upper undivided dyad cell. The same thickened walls as in *balearica*. Fig. 6 I, finally, is an example of the fact that attempts at division may occur also in the upper dyad cell. A clear anaphase is observed, but no indication of a wall. The plasma shows signs of disorganization. In this species, as well, I have only seen triads. Also *Sarcococca humilis* and *Buxus sempervirens* sometimes retard, or inhibit, the division of the upper dyad cell, as will appear from fig. 6 B, E. As to triads in plants, see further

SCHNARF (l. c., p. 102 a. f.). MAURITZON (1933, p. 23) has, later, found similar facts in several species of the *Crassulaceae*.

The tetrad division in *Simmondsia* is brought about when the ovule is in the position shown by fig. 2 I. The apotropous curve is then all but completed, and the integuments on a level with the nucellus, but the place of the ovule in relation to the placenta differs altogether from that of the other species. By this time, the micropyle closes in *Buxus*, but not in other species (fig. 4 E, 3 E, 5 B). The apotropous curve is wholly, or very nearly, completed.

The development of the embryo sac.

So far as I have been able to ascertain, the innermost megaspore develops into E. S. in all species with linear tetrad, and the upper sister cells are absorbed. It is true that several examples of more or less advanced upper tetrad cells have been noticed, but I have not found any case of an upper tetrad cell giving rise to an E. S. Fig. 5 I, for instance, shows a tetrad in *Buxus sempervirens*, in which the two inner megaspores have attained an equal degree of development, whereas the outer two show absorption. Fig. 6 L represents a tetrad in *Pachysandra procumbens*, in which it might have been expected that a micropylar cell would be in process of developing into an E. S. Fig. 6 K is a case in *Simmondsia*, where the chalazal cell had decidedly the upper hand, but where the micropylar one has also had a tendency to further development. In *Buxus sempervirens* as well, I have seen similar tetrads.

The primary E. S. nucleus seems always to have its place in the centre, or in the upper part, of the sac, not in the lower part of it. Before the nucleus proceeds to division, the cell grows, under vacuolization, and continues growing, in the course of the nuclear divisions. See, as to this, the figures representing 1-, 2-, and 4-nuclear sacs of *Buxus balearica* (fig. 6 G, 8 A, B), and *Simmondsia* (fig. 6 K, 7 G, H) designed on the same scale.

The divisions and the wanderings of the nuclei proceed normally, deviations having been observed only in a few cases. In the 2-nucleate stage a normal polarity sets in, and remains. In *Pachysandra procumbens* and *Sarcococca humilis*, a lesser degree of polarity has been observed (fig. 6 B, 7 M). The placing of the nuclei seems to depend upon the amount of space: in the upper pole, which is the wider one, they most frequently lie alongside each other, in the chalazal pole more often above one another, where the sac is getting narrower. A large vacuole takes up the middle part of the sac. The figures 6—8 show the development of the sac in different species. I have seen all the stages in all species except *Buxus Wallichiana* and *Sarcococca zeylanica*. The division, as a rule, takes place synchronously. In *Buxus microphylla*, however, I have, besides, observed asynchronous division, as seen from fig. 8 I. The micropylar nuclei were in advance in meta- or anaphase, the chalazal ones in prophase. As is often the case, the spindles are at right angles in the upper group.

The result of the three divisions is an 8-nucleate E. S. of the normal type. Such cases, with the nuclear groups still undifferentiated, have been observed in the majority of the species (see fig. 7 C, F, 8 F, K). Cell formation soon sets in in both poles, in some cases not quite simultaneously, for instance in *Buxus*

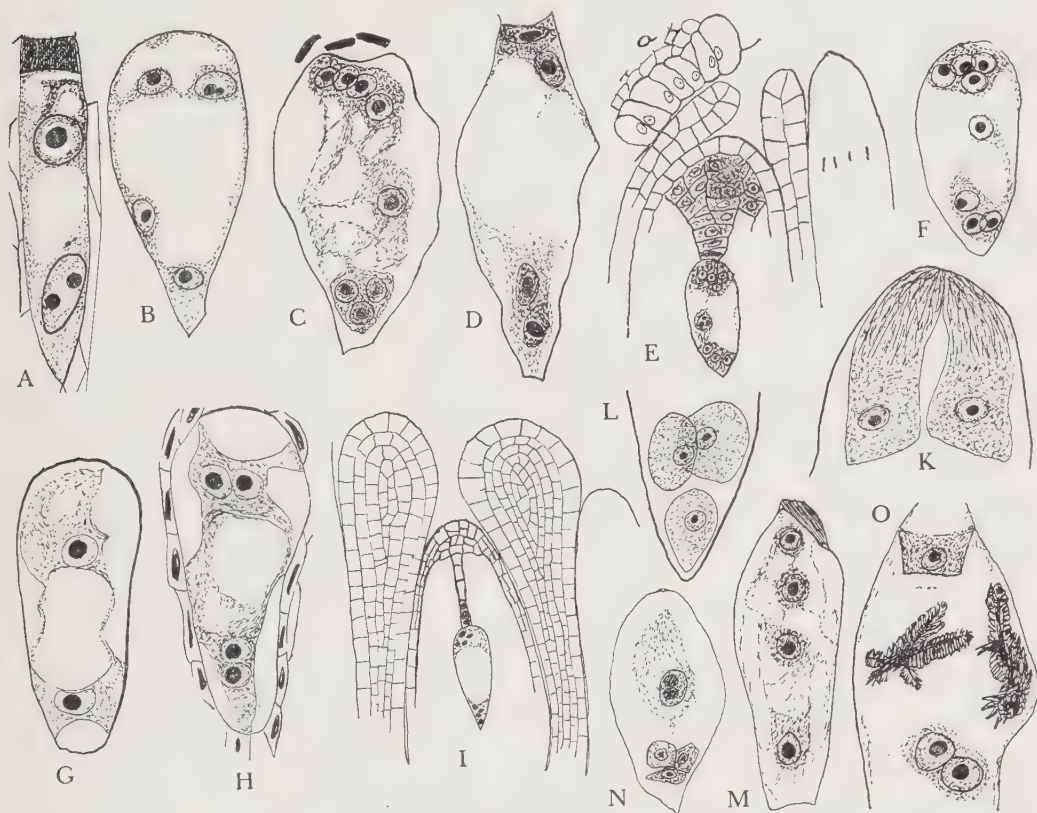


Fig. 7. A-B *Sarcococca pruniformis*. A 2-nucleate E. S. $\times 600$. B 4-nucleate E. S. $\times 340$. C *Sarcococca Hookeriana*. 8-nucleate E. S., remnants of the upper megaspores. $\times 300$. D-E *Sarcococca ruscifolia*. D 4-nucleate E. S. $\times 485$. E 8-nucleate E. S., embryo initials in the nucellus point, obturator (o). $\times 185$. F *Sarcococca humilis*. 8-nucleate E. S., lower pole nucleus has wandered upwards. $\times 400$. G-L *Simmondsia californica*. G 2-nucleate E. S. $\times 600$. H 4-nucleate E. S. $\times 600$. I 8-nucleate E. S., nucellus cap, integuments. $\times 185$. K Synergids with strongly developed »Fadenapparat«. $\times 600$. L Antipodals. $\times 600$. M-N *Pachysandra procumbens*. M 4-nucleate E. S. $\times 600$. N Primary endosperm nucleus and antipodals. $\times 300$. O *Pachysandra terminalis*. E. S. with polar nuclei and pennula-shaped crystals. $\times 485$.

microphylla, the micropylar end of the sac being somewhat advanced, as was also the case with the nuclear division in this species (fig. 8 M). The cell formation is to a certain extent illustrated by fig. 8 L. All four nuclei were found in the same section, but on a different level, two by two. An indication of plasma division is present, the upper two being separated from the lower. Such earlier

cell formation seems to have been observed less frequently in the micropylar pole than in the chalazal one (SCHNARF, l. c., p. 125). STENAR (1925, p. 31) has, however, seen it in *Malva heterophylla*.



Fig. 8. *A-D Buxus balearica*. *A* 2-nucleate E. S. $\times 600$. *B* 4-nucleate E. S., one of the chalazal nuclei not designed. $\times 600$. *C* E. S. $\times 400$. *D* Egg apparatus and primary endosperm nucleus. $\times 400$. *E-G Buxus sempervirens*. *E a-b* 4-nucleate E. S. $\times 1030$. *F* 8-nucleate E. S., the polar nuclei have started moving. $\times 485$. *G* E. S. with the polar nuclei in contact, one antipodal in next section. $\times 485$. *H-N Buxus microphylla*. *H* 2-nucleate E. S. $\times 600$. *I a-b* 4-nucleate E. S. with retarded development in chalazal pole (*b*). Some 30 very small chromosomes could be distinguished. $\times 1030$. *K* 8-nucleate E. S. $\times 300$. *L* Commencing cell formation in micropylar extremity of E. S. $\times 830$. *M* Micropylar pole of E. S. further advanced in development. $\times 485$. *N* The antipodals have divided. $\times 600$. *O-S Pachysandra terminalis*. *O-R* 2-nucleate, 4-nucleate, and ready built E. S. *O-P* $\times 600$, *R* $\times 400$. *S* The antipodals have divided. $\times 485$.

Fully developed embryo sacs are seen in the figures. Fig. 8 G shows an almost ideal section in *Buxus sempervirens*, where the microtome knife has hit no less than seven nuclei at a single stroke. The sac is typical. The smaller size of one of the polar nuclei is no doubt due to a cutting-off, for in other cases they have been of the same size (fig. 8 F). Fig. 8 C shows a sac in *Buxus balearica*,

which is just as typical. The lateral insertion of the egg cell was clearly visible. The antipodals lie beside each other, and the polar nuclei meet in the lower part of the sac. Also in *Pachysandra terminalis* I have seen the lateral insertion of the egg (fig. 11 D). Fibre apparatus («Fadenapparat») in the synergids has been observed in most of the species, and especially in *Simmondsia*, where as much as half of the cell may be seen occupied by a fibrillous, green- coloured substance (fig. 7 K). I have also seen what is termed »Haken» and »Leisten», e. g. in *Sarcococca pruniformis* (fig. 9 C). They are doubtless nothing but some remnants after the cells have become disengaged in conjunction with the degeneration of the egg apparatus, and are probably »ohne jede physiologische Bedeutung» (DAHLGREN 1928, p. 441). STOLT (1921, p. 17) says, speaking of *Gentiana campestris*, that these lists appeared in early stages. In *Sarcococca* and *Simmondsia* I found them mostly in advanced, degenerating embryo sacs, and such was also the case as regards the fibre apparatus. As to these synergid structures, see SCHNARF (1927—29, p. 135 a. f.).

The polar nuclei meet and join at somewhat different points of the sac in the different species (see figures). In *Sarcococca Hookeriana* and *humilis* it seems to be the rule for the lower nucleus to get a start of the upper in its way upwards, as appears from fig. 7 C and F. The fusion has been observed in *Pachysandra terminalis* (fig. 11 B-C), this process consisting in the nuclear membrane dissolving and the plasmas running into one another. Primary endosperm nuclei are given in fig. 8 D and 11 A. Such have been observed in most of the species.

The antipodals are, in this family, three, but they sometimes divide into more (fig. 8 N and S). Their location varies. They remain long vital.

In *Pachysandra terminalis* there occurs in the gynaeceum and in E. S. an abundant crystallization — presumably an oxalate — in the shape of strongly refractive spheres, pennulae, etc., as will be seen from fig. 7 O.

In species with weak nucellus, as *Sarcococca*, *Pachysandra*, and *Simmondsia*, this now begins to be absorbed round the sac (see fig. 7 H). *Buxus*, on the contrary, with its stronger nucellus, shows no such signs of disorganization. Not until now does the micropyle close in *Simmondsia*, *Sarcococca*, and *Pachysandra*. In the first-mentioned genus, the inner integument thickens at the point (fig. 7 I).

The fertilization.

The development above sketched is, in the main, the same in all the genera: in a crassinucellate ovule an E. M. C. undergoes tetrad division, whereupon the chalazal megaspore cell develops into an E. S. of the normal type. By this time the genera start differing somewhat.

The *conductive tissue* is in all species well developed. Fig. 1 E-F, 2 K, 9 A-B, G illustrate this. The stigmata, the insides of the styles, the stylar canal, and the ventral furrows are covered with a papillary epidermis. The cells, especially

those of the styles, are, in later stages, lengthened into something like tubes or flasks, the point gets widened, »key-shaped«, and so on. The plasma becomes thin, and the nucleus is placed in the basal part. Sometimes the cells divide and

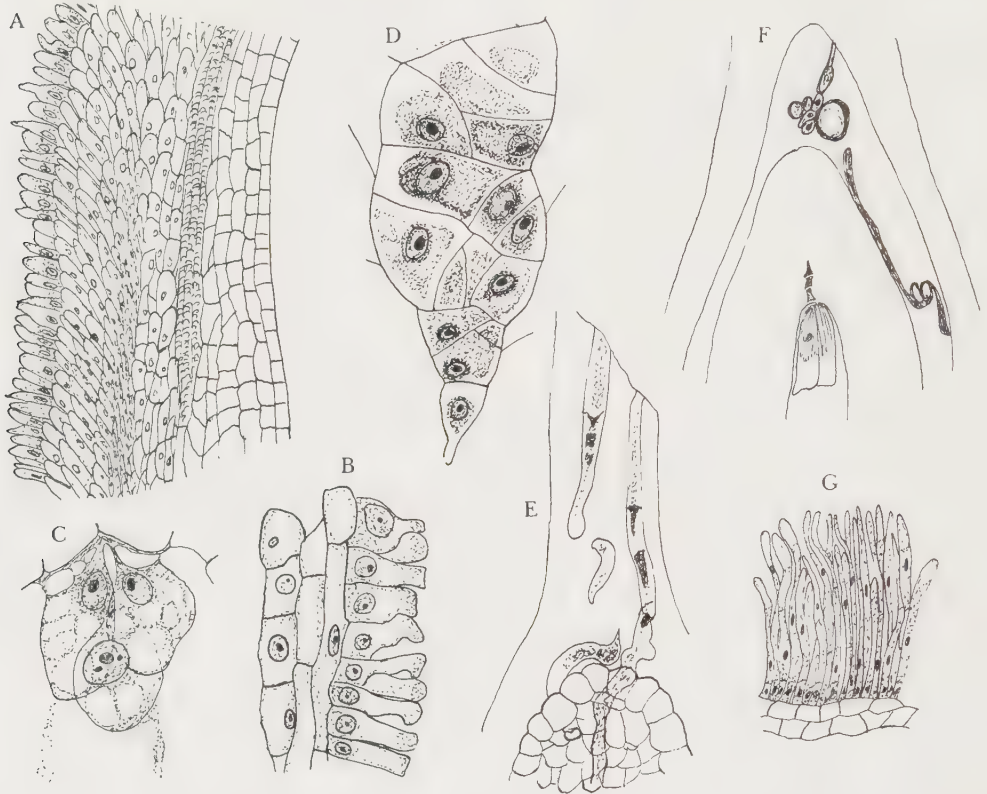


Fig. 9. *A-D Sarcococca pruniformis*. *A* Longitudinal section through style, showing conductive tissue. $\times 90$. *B* Epidermis in stylar canal. $\times 340$. *C* Degenerating egg-apparatus. Point-structure in synergids. $\times 600$. *D* Cellular endosperm. $\times 340$. *E-G Simmondsia californica*. *E* Pollen tubes in micropyle and nucellus, with callus plugs. $\times 300$. *F* Pollen tube has descended between nucellus and integument. Synergids with point structure. Degenerating upper tetrad cells. $\times 185$. *G* Pilosity in stylar canal. $\times 300$.

give rise to club-formed cell bodies. In *Simmondsia* the epidermal cells are, in the stylar canal and on the placenta, lengthened into a long and thick pilosity, at the time of fertilization (fig. 2 K and 9 G).

Below the ectotrophal conductive tissue mentioned in the above paragraph, there is another, endotrophal, consisting of lengthened, more or less plasma-filled cells (fig. 9 A).

All the genera, except *Simmondsia*, have an obturator (fig. 1 I, 4 D, E), formed through periclinal division on the inner side of the funiculus (fig. 3 E). This, too, is later covered by a palisade-like epidermis (fig. 7 E o). An exostome canal is

formed between the obturator and the outer integument. In *Simmondsia* the inner integument is prolonged in the shape of a tube (fig. 12 H).

It is only in *Buxus* and *Simmondsia* that sure signs of fertilization have been noticed: pollen germination on the stigmata, pollen tubes in the gynaecium, disorganized synergids, or sperm nuclei in the E. S. Germinating pollen grains have been observed in *Buxus*; not, however, in *Simmondsia*, whose stigmata seem to wither rapidly in the dry climate where it grows. Pollen tubes in style and micropyle, or in nucellus, have been observed in both genera. Fig. 9 E shows two tubes in the micropyle of *Simmondsia*. The callus plugs appear quite clearly. Porogamy is prevalent in this as well as in *Buxus*. Another instance of micropylar tubes in *Simmondsia* is given in fig. 9 F. The tube has, it seems, failed to find its way into the nucellus; instead it has, after winding into a ball and swelling, descended between the nucellus and the integument. The three nuclei lay in the ball, above the nucellus. The E. S. was evidently in a state of disorganization. The synergids were as much as half filled with a green-coloured fibrillous structure. Disorganized synergids have been observed both in *Buxus* and in *Simmondsia* (fig. 10 A, G, 12 D-E), but I have not, with certainty, seen the male nuclei in the E. S. (Most probably, however, the bodies just below the egg cell in fig. 10 A were really the two sperm nuclei.) In fig. 10 A appeared a round, black body in the chromophile mass in the point of the E. S., probably the nucleus of the degenerated synergid. The polar nuclei had not yet coalesced. There is no cause for doubting double fertilization in these genera. In *Buxus sempervirens* and *microphylla* fertilization seems to occur but rarely in our country. As out-of-door plants they are here on the very boundary of their distribution, wherefore the climate is surely, even in the south of Sweden, unpropitious for sexual reproduction. Of the former plant I have cut several hundreds of ovules, but indications of fertilization or embryo were found only in about two per cent. In unfertilized embryo sacs the egg apparatus degenerates, but the endosperm nucleus divides nevertheless and originates an ephemeral endosperm. *Buxus balearica*, which is, in our parts, an indoor plant, has shown better results, but also in this species many ovules remain unfertilized. Besides, these *Buxus* are more or less protandric, so that the pollen is spread before the E. S. is ready-formed.

The *Sarcococca* and *Pachysandra* have not shown sure signs of fertilization. In one or two cases I have, however, seen a body similar to a pollen tube in nucellus and in E. S., in *Sarcococca pruniformis*, of which I have had an abundant material. Fig. 10 N shows a hypha point in the E. S., which, however, had the appearance of being unburst. No sperm nuclei could be detected. The egg cell was, besides, disorganized and lay free below the synergids, which appeared wholly intact. Eight endosperm nuclei were found in the E. S. These conditions must be deemed to speak against fertilization. The upper cell designed in fig. 11 E might possibly represent a fecundated egg cell in *Pachysandra terminalis*, but no traces of pollen tube could be detected, and the synergid nuclei persisted, although the cells were vacuolized and degenerating, as was, by the bye, also

the egg cell. As regards *Sarcococca* and *Pachysandra*, my material yielded no instance of embryo formation from the egg.¹ *Sarcococca*, at least *pruniformis*, is markedly protandric. The stamens open a couple of months before the E. S. is ready built.

At the disorganization of the egg apparatus in these unfertilized embryo sacs, the egg seems to be the first to be attained. It gets detached from the sac wall, the plasma is vacuolized, the nucleus leaves its normal place and gets hypertrophied, and the nucleolus disintegrates in smaller grains. Later on, the synergids, too, are detached and pass through the same process of degeneration. The E. S. gets hypertrophied, as well as the nucellus round it. Fig. 9 C, 13 A show examples of the above-mentioned disorganization process in *Sarcococca pruniformis*.

The endosperm.

The endosperm in *Buxus sempervirens* was studied by SAMUELSSON (1913, p. 136), who found it to be ab initio cellular. This statement is corroborated by my investigations. At the division of the primary endosperm nucleus, a wall is at once formed in *Buxus* and *Pachysandra*, as a rule crosswise, so that two cells arise, one above the other (fig. 11 D). For the most part these cells seem to be cross-divided once more, at least if the E. S. is narrow (fig. 11 E). Also SAMUELSSON declares, as regards *Buxus sempervirens*, that four endosperm cells, in a row, arise before walls are formed lengthwise (l. c., p. 175). Fig. 10 B shows an instance in this species. Other cases, however, may occur. Thus, in *Buxus sempervirens*, I found the following development in a sac probable (see fig. 10 C): primarily formation of a basal cell, then of a top cell, whereupon the middle cell has split up, in the way the figure shows. Fig. 10 H is an example of early longitudinal division of the upper cell in *Buxus balearica*. Fig. 10 I, K, 11 F, 12 A, C show other instances of cellular endosperms in *Buxus* and *Pachysandra*.

It is evident that the first divisions in the endosperm in these plants is independent of the fertilization, as in several cases the egg apparatus was more or less disorganized or completely absorbed. Many endosperm cells, however, seem

¹ From the Botanic Garden of Copenhagen I have, however, thanks to the ready courtesy of Mr. A. Lange, curator, obtained two fruits of *Pachysandra terminalis*, which I have cut. These had come from Japan, where the plant grows wild. They contained each two seeds with normal embryos and abundant endosperm, as in *Buxus* (fig. 12 I). As I have not managed to obtain any fresh, fixed material of the plant in question from Japan, I cannot state anything definite as to the embryo development, but it may be presumed that it is, there, of normal sexuality. — I should add perhaps that Mr. Lange, at the same time, gave the information that the *Pachysandra* species has never developed any fruits in the Botanic Garden of Copenhagen.

Earlier authors, too, have remarked on the want of fruits in *Pachysandra*: »Fructus desiderabantur» (BAILLON 1859, p. 57), »fructus tricoccus . . . mihi haud obviis, ex cl. Baillon cum iis Buxi conveniens» (MÜLLER, DC. Prodromus). Also VAN TIEGHEM (1897, p. 333) mentions the lack of fruit in that species.

not to be formed until the process in the E. S. is ended. Such ovules abort in *Pachysandra*, but in *Buxus* they often develop and reach the same size as fertilized ones (parthenocarpy, see below).

Sarcococca and *Simmondsia* differ from the above genera, as to the endosperm, in that they form a nuclear one.



Fig. 10. *A-F Buxus sempervirens*. *A* Necrotized synergid. $\times 600$. *B-C* Endosperm in unfertilized embryo sacs. $\times 100$. *D* Parthenocarpic, *E* normal seed, *n* nucellus. $\times 7$. *F* Embryo. $\times 300$. *G-L Buxus balearica*. *G* Pollen tube in E. S. $\times 400$. *H* 3 almost empty endosperm cells, egg apparatus degenerated. $\times 100$. *I* Embryo. $\times 185$. *K* Young embryo. Endosperm. $\times 100$. *L* Same embryo. $\times 485$. *M Sarcococca hookeriana*. Nuclear endosperm in mitosis. $\times 185$. *N Sarcococca pruniformis*. E. S. with 8 endosperm nuclei. Egg apparatus in degeneration. Unburst hypha — pollen tube? — enters into E. S. Numerous embryo initials, and dying cells, in nucellus point. $\times 185$. *O Sarcococca ruscifolia*. Nuclear endosperm with commencing wall formation. Nucleus in mitosis. $\times 225$.

The earliest stages that I have observed in *Sarcococca* are seen in fig. 10 M-N. In the former, which was drawn from an unfertilized E. S. of *Sarcococca hookeriana* are seen a few endosperm nuclei in mitotic division. The small chromosomes in the nethermost nuclear plate may, approximately, be stated as 30 in number. The size of the nuclear plate was in this case remarkable. The

lower left hand spindle was divided by three cuttings, $10\ \mu$ in thickness. The egg apparatus in this E. S. was quite disorganized. A number of embryo initials (see below) were seen in the nucellus point. Fig. 10 N is an E. S. of *Sarcococca pruniformis* with eight endosperm nuclei evenly spread and surrounded by their respective plasma portions. As to the »pollen tube» getting into the E. S., see above.

Not until the cell formation begins, does any great number of nuclei develop in this genus. The nuclei distribute themselves along the wall, from which project lists of cellulose between the nuclei. The cell formation seems to start in the upper part of the sac and proceeds down the chalaza. Fig. 10 Ó is taken from the lower part of an E. S. in *S. ruscifolia* where as yet only slight indications of walls are visible. In the upper part the endosperm was cellular. By degrees the E. S. fills with endosperm tissue (fig. 9 D). The endosperm formation in *Sarcococca* is quite independent of fecundation. In none of the embryo sacs mentioned was there any egg embryo. The egg apparatus was disorganized, but the antipodals subsisted. In the nucellus point, embryo initials were observed (fig. 10 N).

A nuclear endosperm exists also in *Simmondsia*. The earliest stage that I have seen had already 64 nuclei (fig. 12 D). The embryo here contained 13 cells. Also the next stage, 128 nuclei, has been observed (fig. 12 E), with an embryo of 18 cells. Even thus far, the nuclei probably divide synchronously, but later on the division takes place in a wave-like manner, from the micropylar to the chalazal end. The nuclei lie, in *Simmondsia*, more agglomerated in the upper part of the sac, but in the lower only in a thin layer of wall plasm. The upper nuclei are notably larger, rounded, the lower more or less flattened. A similar agglomeration of the endosperm nuclei around the embryo is mentioned by several authors, e. g., HÅKANSSON (1923, p. 42 and 57), STENAR (1925). Mitotic division has been ascertained also in *Simmondsia*. Fig. 12 F shows a later stage of development. The E. S. occupies the larger part of nucellus and reaches down into the chalaza. I have tried to count the nuclei in this sac, and arrived at the number of more than a thousand. It might be presumed that the exact number is 1024, i. e., ten divisions had occurred. In this sac certain nuclei presented, to some extent, an asynchronous division.

The development of the endosperm now sketched happened in *Simmondsia* within a couple of weeks. After another week, the cell formation had begun, and the embryo had assumed the shape that is shown in fig. 12 G. Having been in a position to study, somewhat closely, the progress of the cell formation in the endosperms in this species, I will here give a short account of it, referring to fig. 11 G-K, designed from one and the same E. S. We then find that the cell formation passes off successively from the upper to the lower part of E. S. in connection with a wave of nuclear division. In fig G, drawn from the upper part of the sac, the cell formation is quite completed. Fig. H is from the middle of the sac. The nuclei are gathered in groups, surrounded by thin walls, distinguishable under strong magnification. Between the nuclei, plasma strands are visible, and

also cell plates, in the manner we know from wall formations in nuclear endosperms. Fig. K is a continuation of fig. I, from the lower part of the sac,

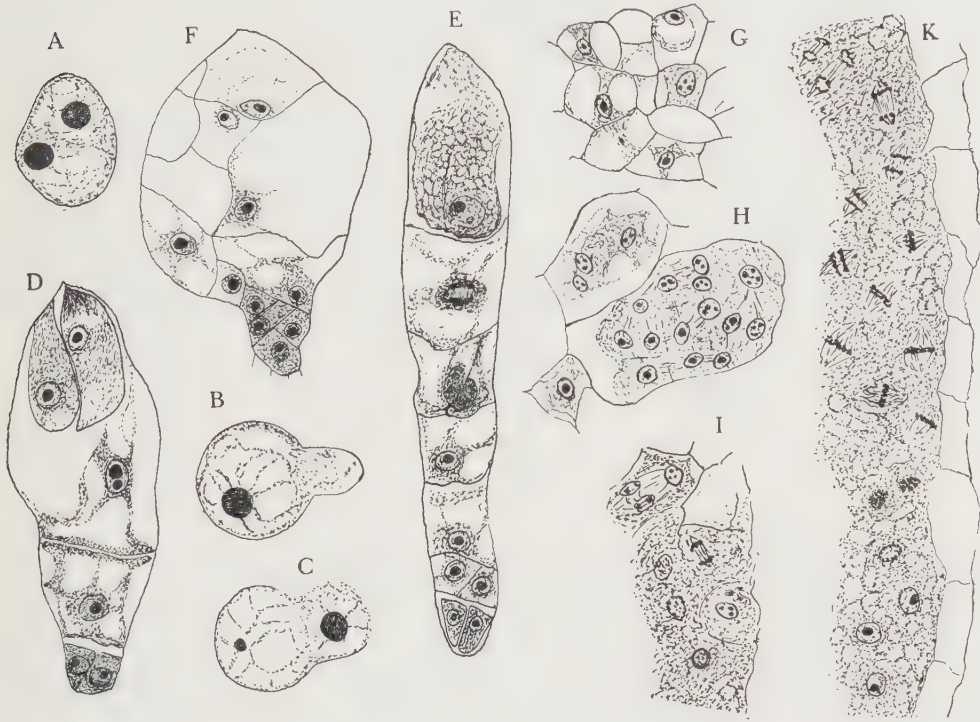


Fig. 11. *A-E Pachysandra terminalis*. *A* Primary endosperm nucleus. $\times 600$. *B-C* Fusion of polar nuclei, two consecutive sections. $\times 600$. *D* 2-cellular endosperm. Lateral insertion of the egg cell visible. $\times 300$. *E* Endosperm. $\times 300$. *F* *Pachysandra procumbens*. Endosperm. $\times 300$. *G-K* *Simmondsia californica*. Nuclear division wave and cell formation in endosperm. See text. $\times 300$.

in which the endosperm only consists of a wall layer. We here see how the nuclear division proceeds towards the chalaza, accompanied by wall formation. From the top (*I*) and downwards we find: recently ready built nuclei, telophases, anaphases, metaphases, one nucleus in prophase, and, finally, three quiescent nuclei. Lower down in the chalaza only such quiescent nuclei were found. One gets the impression that some stimulating fluid—hormon—pervades the wall plasma. I have tried to fix the number of chromosomes, and have found them to be about one hundred, but as they are exceedingly small and numerous, this statement of mine should be regarded as only an approximative one. If, with good reason, we presume double fecundation in *Simmondsia*, and accordingly triploid endosperm nuclei, the haploid number would, thus, be about 35.

A similar process of nuclear division has been observed by several authors, among others by STRASBURGER in *Fritillaria imperialis* (1880), by ERNST in *Tulipa*

Gesneriana (1901, p. 59), by ANDERSSON (1931, p. 30) in *Evonymus latifolius*. The latter author says, also, that the cell formation in the species mentioned and in *Evonymus europaeus* commenced in the micropylar extremity of the sac (l. c. 31). The reversed order, viz., from chalaza to micropylar end, is mentioned by, e. g., STRASBURGER, for *Reseda odorata* (1910, p. 78). See also SCHNARF (1929, p. 325).

It seems probable that, in *Simmondsia*, the cell formation never comes to extend quite down into the chalaza, but that, before this can take place, the plasma layer gets absorbed. Even in the later stages there are free endosperm nuclei in the nethermost part of the E. S., if any plasma then remains (fig. 12 H).

The cell formation in *Simmondsia* proceeds in conformity to HEGELMAIERS (1885) »einseitig-peripherischer Typus«. About its extension, see SCHNARF (l. c., p. 334).

The endosperm in *Simmondsia* contains no reserve nutriment, wherefore this is lacking in the seeds (PAX, 1896).

The embryo. Parthenocarpy in *Buxus*.

As has been mentioned in the preceding chapter, unfertilized ovules in *Buxus* often continue growing, and then attain the same size as fertilized and embryo-producing ones. This holds good at least of *sempervirens* and *microphylla* but probably also of *balearica*. Here, thus, we have partial parthenocarpy. Fig. 10 D-E show a seed of either kind in *B. sempervirens*. They are of the same size and shape. The parthenocarpic one has an exceedingly small E. S. with perhaps 4 or 5 empty endosperm cells. The upper part of nucellus is beginning to shrivel. The normal ovule had a vital E. S. with ditto endosperm and embryo.

In *Buxus balearica*, older ovules have, as a rule, contained an embryo (fig. 12 C). However, I have seen that this species, too, forms a few-celled endosperm without fertilization. These species develop, as appears from fig. 10 F (*B. sempervirens*), a proembryo of a few cells in a row, before the apical cell divides longitudinally. The development follows the *Capsella* type (SOUÈGES 1919, SCHNARF 1928, p. 398). A rather large upper cell exists, as for instance in fig. 10 L. In this embryo the apical cell had, by means of two length divisions, given rise to four cupola cells. These divide crosswise and give rise to an octant of two layers with four cells in each, as appears from fig. 10 I. The outer four form the cotyledon region. They have in this embryo, by means of periclinal walls, already detached one outer dermatogenetic cell each.

The earliest embryo stage I have observed in *Simmondsia* is seen in fig. 12 D. The embryo consisted of 13 cells, and the endosperm of 64 nuclei. A somewhat later stage is given in fig. 12 E, where the embryo contained 18 cells, and the endosperm 128 nuclei. As I have not had any earlier stages at my disposal, I cannot give an exact statement about the embryo type of this species (SCHNARF

1928, p. 397), but to judge by the embryos here mentioned, it does not seem to be the same as in *Buxus*.

In both genera the embryo then differentiates in a suspensor of varying length and embryo globule. Fig. 12 A, C, F-G show later stages. *Buxus* has a short, *Simmondsia* a somewhat longer suspensor. In fig. 12 G the cotyledons begin to come out. The suspensor had, in this case, a thickness of three cell layers.

Fig. 12 H is a section through a seed of the same genus, in which the cotyledons are more prominent. The upper part of the E. S. holds a weak and meagre cellular

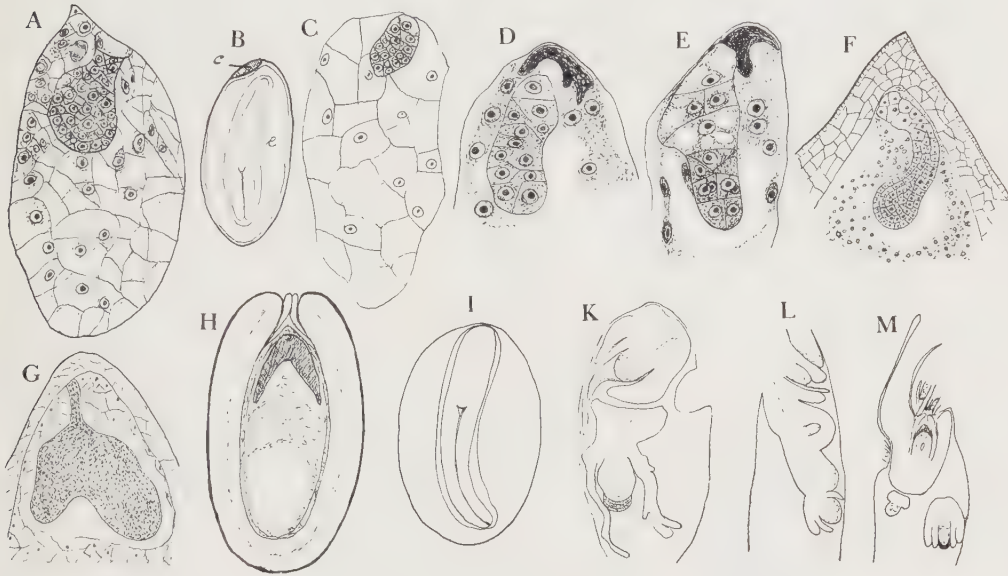


Fig. 12. A-B *Buxus microphylla*. A Embryo and endosperm. $\times 225$. B Seed with embryo. c caruncle, e endosperm. $\times 5$. C *Buxus balearica*. Embryo and endosperm. $\times 135$. D-H *Simmondsia californica*. D-E Embryos and nuclear endosperm, necrotized pollen tubes. $\times 225$. F-G Later embryo stages. F $\times 80$, G $\times 50$. H Seed with older embryo. Endosperm nuclei still free in chalazal end of E. S. $\times 7$. I-M *Pachysandra terminalis*. I Seed with embryo. $\times 6$. K-M Longitudinal section of ovary with abnormal ovules, in M also a normal one. $\times 25$.

endosperm. The chalazal part still contains a thin stratum of wall plasm with free nuclei. Mature embryos in *Buxus sempervirens* and *microphylla* are of the same appearance, except that the hypocotyl of the latter is about twice the size of the cotyledons (fig. 12 B), whereas they are of the same length in the former. Fig. 12 I is a section through a mature seed of *Pachysandra terminalis* from Japan (see above). The embryo in *Simmondsia* is described by VAN TIEGHEM (1897, p. 298): »Sous un mince tégument rouge brun ... cette graine a un gros embryon droit, à racicule supère, à cotyledons plans convexes, épais et oléagineux sans trace d'albumen». He adds that the embryo is eaten fresh or roasted (»Cacao des Papagos»). The other genera have abundant reserve nutriment both in endosperm and embryo.

The nucellar embryony in *Sarcococca*.

ORR (1923) discovered that seeds of *S. ruscifolia* contained several embryos and expressed the supposition that they did not arise in the E. S.¹ Later on, I myself (1930) published the result of a study on *S. pruniiformis*, in which I made it clear that this species, too, has polyembryony, and that the embryo formation starts in nucellus. I also pointed out that this embryo formation must be regarded as quite autonomous, i. e., without any influence from the other sex, as fecundation fails in this plant. And from the following lines it will appear that such vegetative, extra-saccal embryo formation is, in fact, characteristic of this genus. I have observed it also in *Hookeriana* and find a probability for it in *humilis* and *zeylanica* as well, although my material has not comprised all stages of these.

The process of development is, in the main, the same in the different species and proceeds in the following way.

At the period of the completion of the E. S., some cells in the nucellus point assume an archesporial appearance, in that they grow out, get a denser plasma, larger nuclei and nucleoli. The figures 7 E, 13, 14 A show typical stages in four species (cf. also WIGER 1930, fig.). The most important part of the process in the ovule now becomes located to the nucellus point. The E. S. gets hypertrophied, as well as the nucellus around it. The egg- and the antipodal-apparatus begin to show signs of degeneration, whereas the polar nuclei remain vital. The above mentioned cells in the nucellus point are embryo initials. They lie spread all over the point, and, exceptionally, down the upper sides of the sac, and none of them seems predestinated to the rôle of embryo initial. What incitation causes their activity is as yet unknown. That this adventive embryony is secondary, and that, accordingly, these plants have been originally of normal sexuality, would seem obvious. HABERLANDT (1921), has brought forward a theory for the explaining of adventive embryony, and apomixis generally, viz., that from dying cells a »Nekrohormon» spreads, acting as a stimulant on the surviving ones. He even, by inflicting small wounds, contrived to cause adventive embryony, in *Oenothera Lamarckiana*. The experiments, however, were not carried on to the point of developing mature embryos. It may of course be difficult to prove this necrohormon theory, but so far at least HABERLANDT is in the right, viz. that in such cases dying cells are always to be found (see figures). There is no getting away from the impression that the initial cells grow at the expense of the perishing ones. And, indeed, it stands to reason that the nutriment cannot suffice for the further growth of all the cells. Some of them must be sacrificed.

In many plants with adventive embryony, e. g., *Funkia ovata*, *Citrus Aurantium*, *Coelobogyne ilicifolia*, *Mangifera indica*, *Evonymus latifolius*, and *Nothoscor-*

¹ Mr. Orr has kindly furnished me with fixed material of this species, from the Royal Botanic Garden of Edinburgh, for which courtesy I here beg to proffer my thanks.

don fragrans, according to STRASBURGER (1878), the embryos always form in the immediate neighbourhood of the E. S., mostly round the egg-apparatus. This is by no means the case in *Sarcococca*. On the contrary, in this genus it is the cells



Fig. 13. A-B *Sarcococca pruniformis*. A Embryo initials in nucellus point. E. S. and nucellus hypertrophying, egg apparatus degenerating. $\times 340$. B Free embryo in different aspects. $\times 4$. C-D *Sarcococca Hookeriana*. C Initial cells. E. S. still vital. $\times 300$. D Young nucellar embryos. $\times 185$. E-F *Sarcococca ruscifolia*. E Nucellar embryos, E. S. = embryo sac. $\times 300$. F Growing nucellar embryo, E. S. = embryo sac. $\times 300$.

lying farthest up in the nucellus point that appear most vital, as the figures show. It has been found that some of the above mentioned plants stand in need of pollen stimulus for the development of adventive embryony, while others do not; as for instance *Coelobogyne*. ERNST (1918, p. 452) points out that »eindeutige Beziehungen zwischen Entstehungsort der Adventivembryonen und den Vorgängen der Befruchtung sind noch nicht sicher festgestellt worden. Das Wesen der stimu-

lativen Nucellarembryonie scheint aber immerhin die Entwicklung der Adventivembryonen in der Umgebung des Eiapparatus, also dem Orte des unmittelbarsten Reizwirkung, zu begünstigen». As has been said above, there occurs no pollen stimulation in *Sarcococca*. In such plants, thus, the rise of the embryo initials is no doubt less dependent on the E. S. We see, therefore, that in *Sarcococca* they arise farther away from the sac.

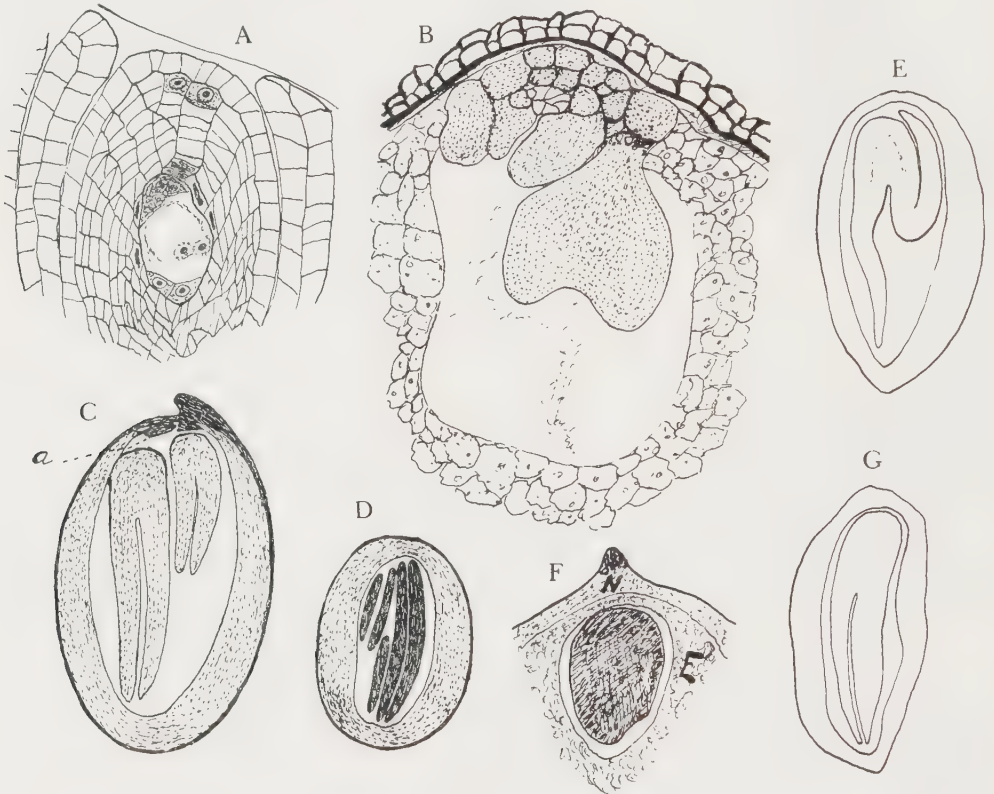


Fig. 14. *A Sarcococca humilis*. Two initial cells. Embryo sac. Upper tetrad cells, and nucellus round the E. S., degenerating. $\times 300$. *B-D Sarcococca pruniformis*. *B* Packet of nucellar embryos in different stages. Endosperm cellular. $\times 80$. *C* Length-, *D* Cross-section of seeds with two and three embryos respectively. *a* abortive embryos. *C* $\times 7$, *D* $\times 6$. *E Sarcococca Hookeriana*. Seed with embryo, one cotyledon has grown backwards. $\times 7$. *F-G Sarcococca zeylanica*. *F* Young embryo, probably a nucellar one. Abortive initials in nucellus point (N), E=endosperm. $\times 30$. *G* Seed with embryo. $\times 7$.

The number of initials in the same ovule may amount to a hundred, or more.

After a period of growth the initials begin to divide and give rise to rounded cell bodies, embryos, enclosed within the original wall (fig. 13 D-E). Later on they are seen agglomerated into something like a little packet; not all of them are equally advanced (fig. 14 B). It would seem clear that it is, in the first place, the embryos lying nearest to the E. S. that come to further development, whilst

the others — for lack of nutriment, or for other reasons — abort. HABERLANDT (1921) has suggested that specific »embryobildende Hormone» might exist in the E. S. This hypothesis is supported by an observation that I have made: the growth of the embryos accelerates, as soon as they approach the E. S. Fig. 13 F shows such an embryo; it has just got into touch with the E. S. and entered upon a decided elongation. Of the embryos, the majority abort, so that only one, two, or, at most, three, ripen. HEGELMAIER found in *Euphorbia dulcis*, which greatly resembles *Sarcococca* in this respect, in 75 % of the seeds, 2—3 developed embryos, besides a great many abortive ones. Fig. 14 C-D show sections through mature seeds with respectively two and three embryos, somewhat unequally advanced. An exposed embryo is shown in fig. 13 B. The cotyledons are round. The endosperm and the embryos contain abundant reserve nutriment. The nucellar embryos resemble, upon the whole, the ovular ones, when ripe. SCHNARF (1929, p. 469) states that the former, however, lack suspensors. They have, as the figures show, a short and thick hypocotyl. My material of *S. zeylanica* has not comprised the earlier embryo stages, but in the point of the ovule drawn in fig. 14 F there were traces of abortive initial cells. Moreover, the shape of the embryo, both in that figure and in fig. 14 G speaks in favour of their quality of nucellar embryos. Also in *Hookeriana*, the development of which has been made clear, the single embryo observed in mature seeds has had the same appearance (fig. 14 E).

Besides the *Sarcococca*, the following plants have been found to have autonomous nucellar embryony: *Euphorbia dulcis* (HEGELMAIER 1901, CARANO 1926), *Coelobogyne ilicifolia* (STRASBURGER 1877—78), *Xanthoxylum Bungei* (LONGO 1908), and some others. The development of E. S. and of embryos bears in these a close resemblance to that in *Sarcococca*.

For further particulars, I refer to authors such as WINKLER (1908) and ERNST (1918), who have devoted special interest to this subject.

The seed.

The nucellus persists temporarily as transitory perisperm, without, however, storing any reserve nutriment (fig. 10 D-E, 15 C). Ultimately it is quite superseded by the endosperm (fig. 14 C-D, 15 A). In all species the nucellus is limited by a cuticle (fig. 15 A-B, E), in *Simmondsia* a rather weak one. The seed testa consists in *Buxus* of the outer integument (fig. 15 C), the inner only appearing in the micropyle (fig. 15 E). In *Simmondsia*, *Pachysandra*, and *Sarcococca*, also the inner integument takes part, with its inner layer, in the forming of the testa (fig. 15 A i). The epidermis of the outer integument consists of palisade-like, thick-walled cells. The hypodermal layer in all genera consists of several small-celled strata, at least 8—10, or more (fig. 15 C) in *Simmondsia* about 20. These strata are later on pressed together, giving the appearance of only three, thick-

walled, layers (fig. 15 A). These observations of mine do not agree with certain remarks of VAN TIEGHEM (l. c. 314) and SAMUELSSON (1913, p. 175) who speak of about three layers of thin-walled, isodiametric cells. Compare, besides, NETOLITZKY (1926, p. 190). In *Buxus* the outer palisade-layer continues into the micropyle (fig. 15 E). *Buxus* has a caruncle (fig. 10 D-E) formed by funicle epidermis and consisting of palisade-cells.

Seldom do all the seeds in the fruit ripen. In *Sarcococca*, for instance, one or two, in *Simmondsia* only one. Fig. 15 G shows the seed column in *Simmondsia* with the three seeds. The rudimentary ovules in *Sarcococca* and *Simmondsia*

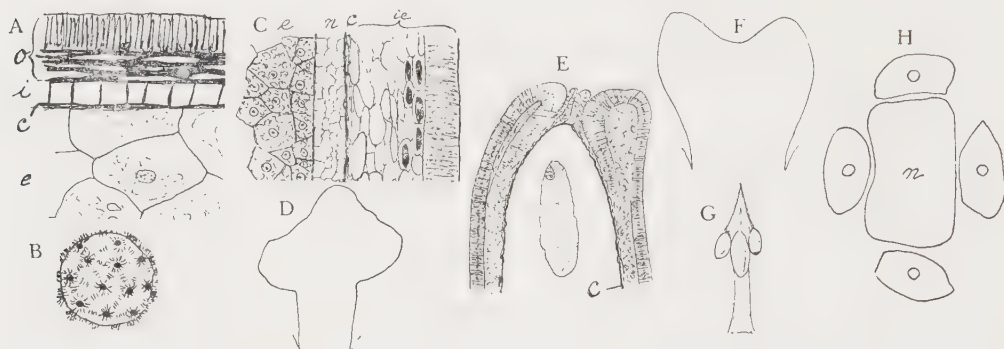


Fig. 15. A-B, H *Sarcococca pruniformis*. A Seed testa. o outer integument, i inner stratum of inner integument, c cuticle, e endosperm. $\times 300$. B Pollen grain. $\times 870$. H Transverse section through filaments and nectary (n) in male flower. $\times 60$. C-D *Buxus microphylla*. C Seed testa. e endosperm, n nucellus, c cuticle, ie outer integument. $\times 90$. D Nectary in male flower. $\times 25$. E *Buxus balearica*. Section through fore-part of seed. c cuticle. E. S. with embryo and endosperm. $\times 25$. F *Sarcococca zeylanica*. Nectary in male flower. $\times 25$. G *Simmondsia californica*. Seed column with one normal and two rudimentary seeds. $\times 3$.

start developing an E. S. in the same manner as the normal ovules, but then their development stops. The polar nuclei have been seen in contact, but I have never observed any endosperm. However, in *Sarcococca*, embryo initials develop in the nucellus point, but no embryos are formed, since the ovules abort.

Abnormal ovules in *Pachysandra terminalis*.

A peculiar development of rudimentary, abnormal ovules, besides the normal ones, has been observed in *Pachysandra terminalis*. Fig. 12 K-M give instances of these abnormal ovules. They begin to appear at the time of the tetrad division in the shape of small plasmic excrescences on the placenta above the ordinary ovule. They grow out one after the other, and not only from the placenta, but from all parts of the wall in the upper portion of the chamber, seldom below the centre. Those sitting on the inside of the funicle often make their way into the

micropyle of the normal ovule, as shown by fig. 12 M. Their number may amount to ten or more in the same partition. Sometimes they sit on incomplete septa, as in fig. 12 L, where no fewer than six small bulbs were placed in a row on one wall list. Even above the placenta I have seen them, in the stylar canal. Their orientation is highly varying, from an orthotropous to a more or less anatropous one. On account of their crowded position they are apt to become somewhat deformed. The funicle is sometimes lacking, sometimes existing only as a long, straight stem. Their size is very variable. Abnormal ovules are at times wanting.

The rudimentary ovules have a nucellus and more or less abnormal integuments. These may appear sometimes as small, basal collars, sometimes as lengthened tubes (fig. 12 K). Often the integuments present additional appendages. The nucellus contains a homogeneous vegetative parenchyma under an epidermis. No archesporium has been observed. A periclinal division in the nucellus-point occurs, as in normal ovules (fig. 12 K).

That this rich collection of deformed ovules has something to do with the lack of sexual reproduction, would seem evident. When the normal ovule is put out of function, the placenta tissue is again brought into play, and then the incitement spreads to other parts of the ovary chamber. The production seems to go on as long as the gynaecium remains on the plant.

It seems impossible that these abnormal ovules should be of any importance at all for the reproduction of the species.

The pollen development.

Buxus, *Sarcococca*, and *Pachysandra* have four episepalous stamens, *Simmondsia* has pentamerous flowers with about 12 stamens. In the first three there is, in the male flower, a so-called rudimentary gynaecium which secretes nectar (see below). The stamens are at first undifferentiated papillas, later on the anther is formed, rather long and dorsifix. I have not studied very closely the development of the archesporium. The wall of the anther has the normal strata, exothecium and endothecium, and, farthest in, a tapetum. Between the last two we have 1—3 thin cell-layers which get absorbed. In *Pachysandra procumbens* the tapetum seems to develop from sporogeneous cells. Fig. 16 A and S show transverse sections through pollen sacs in *Simmondsia* and *Sarcococca*. When, during the tetrad division, the tapetum is at the height of its development, it is frequently many-layered. The cells are plasmic and have, as usual, one or more nuclei. Different degrees of thickness have been observed in *Pachysandra terminalis*, that of the outer side being the thickest. This matter seems to have been but little observed. ROCEN (1927, p. 13), however, found in the *Nyctaginaceae* the tapetum more developed on the side of the sac facing the connective.

No genuine periplasmodium is formed in these plants. In *Simmondsia* the tapetum assumes, in later stages, an appearance reminiscent of a periplasmodium. The cells get hypertrophied, so that the pollen mother cells are squeezed together

into a little group in the centre (fig. 16 A). Or else, the tapetum cells enter between the pollen mother cells, and then the resemblance to a real periplasmodium becomes still stronger. However, as far as I have been able to ascertain, the tapetum cells do not seem to completely relinquish their organization, even though the inside wall sometimes appears to be dissolved.

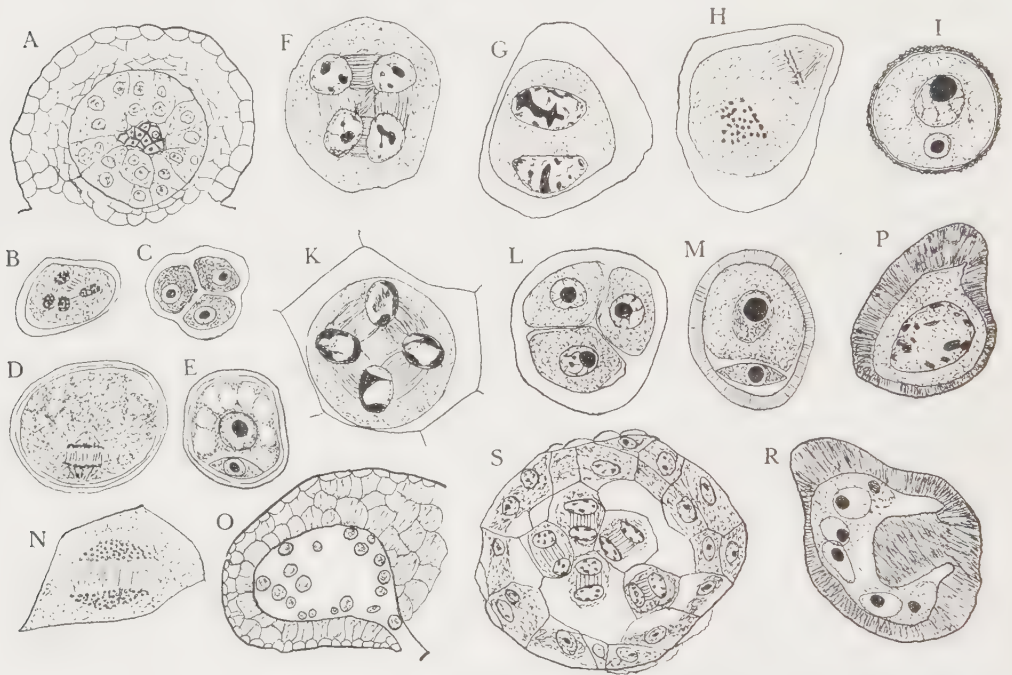


Fig. 16. *A-E Simmondsia californica*. *A* Transverse section through pollen sac. Tapetum cells hypertrophying. $\times 100$. *B* Homotypic division in pollen mother cell. $\times 485$. *C* Pollen tetrad. $\times 485$. *D* Primary nuclear division in pollen grain. $\times 690$. *E* Lens-shaped generative cell formed. $\times 485$. *F Buxus balearica*. Homotypic telophase in pollen mother cell. $\times 830$. *G-I Buxus microphylla*. *G* Interkinesis in pollen mother cell. $\times 900$. *H* Homotypic division in pollen mother cell, about 30 chromosomes, $\times 1030$. *I* 2-nucleate pollen. $\times 600$. *K-M Buxus sempervirens*. *K* Tetrad division in pollen mother cell. $\times 1030$. *L* Pollen tetrad. $\times 1030$. *M* Lens-shaped generative cell detached. $\times 1030$. *N Pachysandra terminalis*. Mitosis in tapetum cell. $\times 900$. *O-R Pachysandra procumbens*. *O* Pollen sac. Pollen grains of different sizes. Fibrous strata. $\times 50$. *P* »Restitution» nucleus in pollen mother cell. $\times 485$. *R* »Furrowing». $\times 600$. *S Sarcococca pruniformis*. Pollen sac with dyad nuclei. $\times 300$.

ROCEN (1927, p. 14) has found something similar in *Oxybaphus nyctagineus* and *Bougainvillea glabra* of the *Nyctaginaceae* and characterizes it as a false periplasmodium. TISCHLER (1908) saw the same thing in *Mirabilis jalapa*. SCHOCH (1920) gives a description of an observation that he made in *Burmannia* which closely resembles what I found in *Simmondsia*. At the period of the pollen-formation »beginnen die Tapetenzellen sich zu deformieren. Ihre Wände erscheinen besonders nach dem Innern des Pollensackes dünn und jeder Festigkeit zu ent-

behren. Bisweilen sind sie sogar ganz unsichtbar, so dass die Vermutung nahe liegt, sie seien völlig aufgelöst ... Oft aber werden die Pollenkörner selbst in das Tapetum hineinverlagert.» On account of such actually existing intermediate forms between the genuine syncytium and the tapeta here described, SCHNARF (1927, p. 34) suggests that these should be termed amoeboid tapeta, as opposed to the ordinary secretional tapetum.

Mitotic cell division has been observed in the anther-tapetum (fig. 16 N). In the course of the pollen-formation, the tapetum gets completely absorbed. The cells loosen and are found lying between the pollen cells in the sac.

In all genera a typical and well-developed fibrous stratum is formed. Sometimes there are several strata, and in the connective as well (fig. 16 O). Compare CHATIN, 1870, pl. XXX.

The nuclei of the pollen mother cells pass through the heterotypic stages and give rise to two dyad nuclei without any wall formation, whereupon a new division results in a tetrad. The pollen formation is, thus, simultaneous. This I have seen in *Buxus sempervirens*, *balearica*, *microphylla*, *Sarcococca pruniformis*, the *Pachysandra* species, and *Simmondsia*. Fig. 16 shows the process. The position of the nuclei in the tetrad seems to vary, even in the same species. Sometimes tetrahedral tetrads are formed, sometimes quadratic ones (fig. 16 C, F, K-L). In a homotypic nucleus plate in *Buxus microphylla* the chromosomes could be fixed at about 30, i. e. the same number as was seen in the E. S. (fig. 16 H).

The wall formation takes place in *Pachysandra procumbens* according to the »furling type» (fig. 16 R; cf. FARR 1916) or »Membranlistentypus» (YAMAHA 1926). A strong wall of varying thickness surrounds the mother cell, from which cellulose lists grow in between the nuclei. The nuclear division seems disturbed, resulting in nuclei of different sizes and later on pollen of similar quality (fig. 16 O). CHATIN mentions and designs some »granulations jaune pâle (comme le pollen) fixées contre la troisième membrane» (1870, 122, pl. XXX), probably dwarf pollen. Sometimes one sees nuclei such as in 16 P, which may be what ROSENBERG (1926—1927, p. 321) calls restitution nuclei. In *Buxus microphylla* as well, I have seen tendencies towards the same wall formation, but also towards cell division of the same type as that of other species investigated, viz., the cell plate type. About the different types, see YAMAHA (1926) and SCHNARF (1927).

By degrees the mother cell dissolves, and the pollen cells become free. They are then 1-nucleate, but soon a lens-shaped parietal generative cell is detached, which has been seen in several species (fig. 16 D-E, M). This cell wanders, in the usual manner, into the vegetative plasma. The mature pollen is 2-nucleate (fig. 16 I; cf. SCHÜRHOFF 1924) and seems normal, except in *Pachysandra* and *Sarcococca*, which have numerous small and plasma-thin grains. KERNER (I, 1896, p. 625) speaks of »zusammenhängenden Pollen» in *Pachysandra procumbens*, which I have not been able to find (fig. 16 O). The pollen is in this family adorned with curious rings and protuberances (fig. 15 B): »grana pollinis stellatim subreticulata» (MÜLLER, D. C., Prodr. XVI, 9).

In *Simmondsia* several of the numerous stamens often fail to produce efficient pollen, as their substance degenerates.

The so-called rudimentary gynaeceum. Ever since ADR. DE JUSSIEU wrote his monograph »De Euphorbiacearum generibus medicisque earumdem viribus Tentamen» (Paris 1824), systematical manuals have mentioned an »ovarîi rudimentum» in the male flower in some of the plants here concerned. DE JUSSIEU, in classifying the Euphorbiaceae, divided them into six sections. The first of these had this rudiment, and to that section were assigned the then known Buxaceae. He describes and even draws three cells observed in it. BAILLON, however, who has a somewhat detailed account of this »corps central», has never seen any cells in this rudiment. He writes (l. c., p. 24): »Le tissu de ce corps central ne rappelle en rien celui du pistil normal. Il est composé de cellules molles dans l'intérieur desquelles sont des gouttelettes huileuses.» The organ, however, is still termed »ovarîi rudimentum» (MÜLLER in D. C., 1869; BENTHAM and HOOKER, *Genera*, p. 266, 1883), or »Rudiment des Fruchtknoten» (PAX 1896). VAN TIEGHEM (1897, p. 307) takes the same position as BAILLON: »Ce corps est dépourvu de méristèles et formé d'un parenchyme homogène et plein, riche en sucres et dépourvu d'amidon . . .». On the surface he has observed »stomates aquifères», out of which dropped a sugary nectar. »On voit donc que ce corps central, regardé à tort par tous les auteurs comme un pistil rudimentaire, n'est pas autre chose qu'un disque nectari-fère» (l. c.).

I have cut the organ in question, in several species, and found it to consist of a »parenchyme homogène», without any trace of ovary chambers. The »stomates aquifères» spoken of by VAN TIEGHEM have also been observed by me, in *Sarcococca pruniformis*. They resemble ordinary stomata in leaves.

There is, then, no cause, here at least, for us to consider this »ovarîi rudimentum» as anything else than a nectary. And besides, if at some epoch, it had really been a pistil, some traces ought to have remained.

The shape of the nectary appears from fig. 15 D, F, H. It exists in *Buxus*, *Sarcococca*, and *Pachysandra*, but not in *Simmondsia*. It is best developed at the opening of the anthers, and is then a pillar-like protuberance about one millimetre high, more or less club-shaped, or widened at the corners.

GOEBEL (Org. I, 1928, p. 184) holds, contrary to VAN TIEGHEM (1897), that the nectaries of both male and female flowers are of the same morphological character, i. e., this so-called rudimentary ovary is, as GOEBEL has it, represented by four interfilamentary protuberances, grown together in the centre.

A word on the place of *Simmondsia* in the system.

Simmondsia californica stands sole in its genus, ever since the shrub was discovered on the coast of California by NUTTALL (1844, p. 400). Its place in the system has, however, been somewhat discussed. The discoverer wrote about his

find: »there is little doubt that this curious shrub belongs to the order of *Garryaceae* Lindl., differing considerably in habit from *Garrya* as well as in inflorescence; the stamens are also more numerous and the ovary more than 1-celled; the disposition of the ovules is the same, and the structure of the seed will prove probably very similar. Our plant is also closely related to the *Putranjiva Roxburgii* of WALLICH».

Later systematists have regarded a coupling together with *Garrya* as untenable. Their observations do not bear out the supposition of the discoverer. Neither the placentation nor the structure of the seed are conformable. See further ENGLER and PRANTL (Nachtr. IV, p. 62) and SCHNARF (1931, p. 30). The affinity to *Putranjiva*, claimed for it by NUTTALL, was better founded, wherefore LINDLEY placed the plant among the *Euphorbiaceae*, proximate to *Buxus*, which place it has since then kept. However, VAN TIEGHEM (1897) took up this question again in his monograph on the *Buxaceae*, laying stress upon the numerous differences between them, e. g., dioecism, pentamerosity, 1-ovular ovaries, lack of reserve nutrition in the seed and of nectaries in the flowers. He found reasons for singling out from the *Buxaceae* and for constituting a new family, *Simmondsiaceae*, which he saw proper to place among the apetalous Centrosperms.

To the above-mentioned morphological deviations from the bulk of the *Buxaceae* my own investigations have now added others of an embryological character; hardly, however, weighty enough to decide the matter. We have seen that the early placentation is somewhat different, basal instead of apical, that the obturator is lacking, and that the inner integument is many-layered, etc. For the rest, the ovule undergoes the same development as in other *Buxaceae*. In its external appearance *Simmondsia* resembles most of all a *Buxus*, and bears hardly any likeness to the Centrosperms. From an embryological point of view, it is true, a coupling together with these might not encounter any serious obstacles, but it may be questioned whether *Simmondsia* would thereby obtain a more natural position than it has already.

Meliaceae.

The tropical family of *Meliaceae* comprises some 40 genera, with about 600 species (HARMS 1896), the embryological development of which has hitherto been but a little known. What has been published on the subject consists in a short account of the later embryo stages and the viviparity in *Carapa moluccensis* LAM. (= *Xylocarpus granatum* KOEN.), by KARSTEN (1891, p. 21) in his study on the mangrove vegetation in the Malayan Archipelago. Besides this, SCHNARF (1931, p. 142) communicates a series of data from some unpublished observations made by Mrs. KRETZKY-DERSCH concerning the development in *Carapa guianensis*. From these we gather that in *Carapa* the pollen mother cells lie in only one row, that they divide simultaneously, and that the anther tapetum is normal; further, as to the ovule, that it is crassinucellate and bitegmic, that an archesporial cell gives rise to a parietal cell, and that the embryo sac develops according to the normal type. The antipodals are insignificant. Porogamy prevails. The endosperm is nuclear.

HARMS divides the family into three sub-families, of which I have, more or less, investigated the following 40 species out of 13 genera:

I. Cedreloideae.	<i>Sandoricum borneense</i> MIQ.
<i>Cedrela Glaziovii</i> C. DC.	» <i>Koetjape</i> MERR.
	<i>Dysoxylum alliaceum</i> BL.
II. Swietenioideae.	» <i>amooroides</i> MIQ.
<i>Khaya senegalensis</i> JUSS.	» <i>Blumei</i> MIQ.
<i>Chukrasia tabularis</i> A. JUSS.	» <i>caulostachyum</i> MIQ.
<i>Swietenia Mahagoni</i> L.	» <i>macrothyrsum</i> MIQ.
» <i>macrophylla</i> KING.	» <i>nutans</i> MIQ.
	» <i>ramiflorum</i> MIQ.
	» spec.
III. Melioideae.	» <i>urens</i> VAL.
<i>Carapa guianensis</i> AUBL.	<i>Chisocheton amboinensis</i> VAL.
<i>Turraea obtusifolia</i> HOCHST.	» <i>divergens</i> BL. var. <i>minor</i>
» <i>floribunda</i> HOCHST.	VAL.
<i>Melia Azederach</i> L.	<i>Aphanamixis grandifolia</i> BL.
» <i>Candollei</i> A. JUSS.	<i>Aglaia angustifolia</i> MIQ.
» <i>floribunda</i> CARR.	» <i>argentea</i> BL.

<i>Aglaia eleagnoidea</i> BENTH.	<i>Aglaia odorata</i> LOUR.
» <i>Eusideroxylon</i> K. & V.	» <i>odoratissima</i> BL.
» <i>eximia</i> MIQ.	» <i>oxypetala</i> VAL.
» <i>Forstenii</i> MIQ.	» <i>rufa</i> MIQ.
» <i>Ganggo</i> MIQ. (f. <i>amboniensis</i> MIQ.).	<i>Walsura pinnata</i> HASSK.
» <i>glabriflora</i> HIERN.	» <i>quadrilocularis</i> VAL.
	» <i>robusta</i> ROXB.

The material was collected in the Botanic Garden of Buitenzorg, Java, with the following exceptions: part of the *Swietenia Mahagoni* material is from Georgetown, British Guiana; some of the *Carapa* material, and *Aglaia glabrifolia*, from the Botanic Garden of Singapore; the *Turraea* species were collected in the Royal Botanic Garden at Kew; *Melia floribunda*, and part of the material used for *Melia Azedarach* and for *Aglaia odorata*, has been collected by J. MAURITZON, Academical Docent, Lund, in the Botanic Gardens of Berlin (*Aglaia*) and Palermo (*Melia*).

Gynaeceum. Genesis, number and orientation of the ovules.

HARMS describes in detail the structure of the flower in this family. A few items may be quoted. A feature that is characteristic of *Meliaceae* is the occurrence of a staminal tube, i. e., the filaments exist connate in a shorter or longer cylinder, in the upper part or brim of which the anthers are fastened. In most cases the staminal tube reaches the height of the style. Other characteristics to be mentioned — common in fact to the whole order of *Terebinthales* — are an intrastaminal disk, resin-, balsam-, or oil-conducting secretion cells, crystals of different kinds, etc. These secretions give much trouble in the cutting of the specimens, where they occur as hard yellow grains which are carried forwards by the knife, thus destroying the cuttings, a trouble no doubt familiar to other embryologists working with tropical material.

About the disk the following at least should be touched upon. It is sometimes altogether lacking, as for instance in the majority of the *Aglaia*, some *Turraea*, and *Aphanamixis*. When existing, it is rather variable in the different genera. In its simplest form, it only consists of an annulus round the basal part of the ovary, as in *Turraea* (fig. 18 D), *Melia* (fig. 17 A), and others. If the annulus grows out horizontally into a carneous border, we get a disk like that in *Khaya* or *Carapa*. If the border bends more or less upwards, we get instead a bowl- or cup-shaped disk, as in *Swietenia* and *Walsura* (fig. 18 A and E). Finally, with this development carried on still further, we find, in certain genera with long, tube-shaped flowers, e. g., *Sandoricum* and *Dysoxylum*, a long, socket-like disk, which surrounds the lower half of the style.

The gynaeceum is, in *Meliaceae*, syncarpous. Its shape is highly varying. As a rule the flowers are small in this family, but occur in copious inflorescences. *Aglaia* especially has very small flowers and ovaries; see fig. 18 B, where the magnification is no less than 70. The carpels vary in number, even within the same species. Usually we find 2—5, rarely only one, as in certain *Aglaia* species,



Fig. 17. A-F *Melia Azedarach*. A Gynaeceum and staminal tube. *d* disk. $\times 20$. B-C Longitudinal sections through young buds, showing the origin of gynaeceum and stamens. $\times 50$. D The origin of the ovules. $\times 140$. E-F Transverse sections through stigma and style. $\times 20$. G *Cedrela Glaziovii*. Transverse section through the upper part of the ovary. $\times 50$. H-L *Chukrasia tabularis*. H-K Transverse sections through stigma, style, and ovary. H-I $\times 20$, K $\times 50$. L Longitudinal section through the placenta. $\times 20$.

or more than 5, as in *Melia* (up to 8), *Turraea* (up to 20). Three is the dominating number in a great many genera, e. g., in the great genus *Dysoxylum* (fig. 18 G), in *Chukrasia* (fig. 17 K), and in *Walsura*. Most of the *Aglaia* have two carpels; in this genus, however, the number varies, between 1 and 4, which latter I have found in *Aglaia Eusideroxylon*. *Cedrela*, and *Swietenia* have a quinate gynaeceum (fig. 17 G).

The shapes of the style appear from the diagrams of the gynaeceum; the style is seldom lacking, as in *Aglaia* (fig. 18 B). In *Aphanamixis* it is very short, in

others particularly long, e. g. in *Dysoxylum* and *Chisocheton*. The stigma is often round, plate- or head-like (*Cedrela*, *Swietenia*, *Carapa*, fig. 18 A), sometimes club-shaped (*Turraea*), or more or less split into lobes, occasionally rather long, but never, in the *Meliaceae*, spreading (figs. 17 A, E, 18 A-B, E). A whorl of long hairs skirts the round and plate-like stigmata (see fig. 26 H). Otherwise the epidermis of the stigmata and of the stylar canal is palisade-like (fig. 26 I).

As to the structure of the gynaceum, see further HARMS (1896).

PAYER (1857, p. 112, 118, and pl. 26) describes the genesis of the gynaeceum in *Cedrela Toona* (= *Toona ciliata*) and *Melia Azedarach*; in the latter as follows: »A l'origine, le pistil se compose de cinq mamelons parfaitement distincts entre eux et superposés aux pétales; mais bientôt ces mamelons grandissent, deviennent connés, et forment un sac dont l'intérieur se partage en cinq compartiments par des cloisons qui, partant des parois de ce sac, se dirigent vers le centre, s'y rencontrent et s'y soudent. Ces cloisons sont alternes avec les mamelons primitifs, au pied de chacun desquels on observe une légère excavation. C'est dans cette excavation, qui ne devient jamais très profonde et qui forme la partie inférieure de la loge, qu'on observe deux ovules qui sont anatropes et ascendants.»

The development in this species is also illustrated by my figures 17 B-D. Fig. B is a section through a young flower bud, with commencing gynaeceum and stamens. In C the ovary is closing, and the carpels are growing upwards, in D the ovules are becoming visible.

These latter originate as small papillae on the turned-in edges of the carpels, in the inner angle of the ovary chamber. As the carpels grow together in the centre, the placentation in the *Meliaceae* is, accordingly, central and marginal. The number of ovules in each chamber varies. In the sub-family *Melioidae*, which comprises $\frac{3}{4}$ of all the genera, there are, with few exceptions, 2 ovules in the chamber (fig. 18 E); *Swietenioideae* (*Khaya*, *Chukrasia*, *Swietenia*, etc.) and also some other genera, e. g., *Cedrela* and *Carapa*, have chambers with several ovules (fig. 17 L, 18 A). We sometimes also find only 1 ovule, as in *Chisocheton* and certain *Aglaia* (fig. 18 B).

In genera with multiovulate chambers the ovules arise acropetally (fig. 18 H), »les plus jeunes étant en haut et les plus âgés en bas» (PAYER, l. c., p. 112). They occur in a row above one another on either edge of the carpel, and vary in number even within the same species. In *Chukrasia* they are particularly numerous. In fig. 17 L no less than 18 ovules may be counted in one row, thus in one and the same chamber about double that number. As this species has, normally, ovaries with three chambers, each flower produces about a hundred ovules. In chambers with two ovules, these have, originally, collateral and basal position. In the course of development, there occurs, in most of the genera with such ovaries, a displacement, so that they come to be more or less above each other (fig. 17 D). A longitudinal section gives the characteristic picture seen in fig. 17 A, 18 F, I. In a few of the genera the ovules remain, all along, in their collateral position, as in *Walsura* (fig. 18 E), *Sandoricum*, and others.

According to the space, the ovules vary considerably in their orientation. If they are allowed to grow quite independently and without hindrance, they assume the epitropous and pendulous position peculiar to the family, with the micropyle

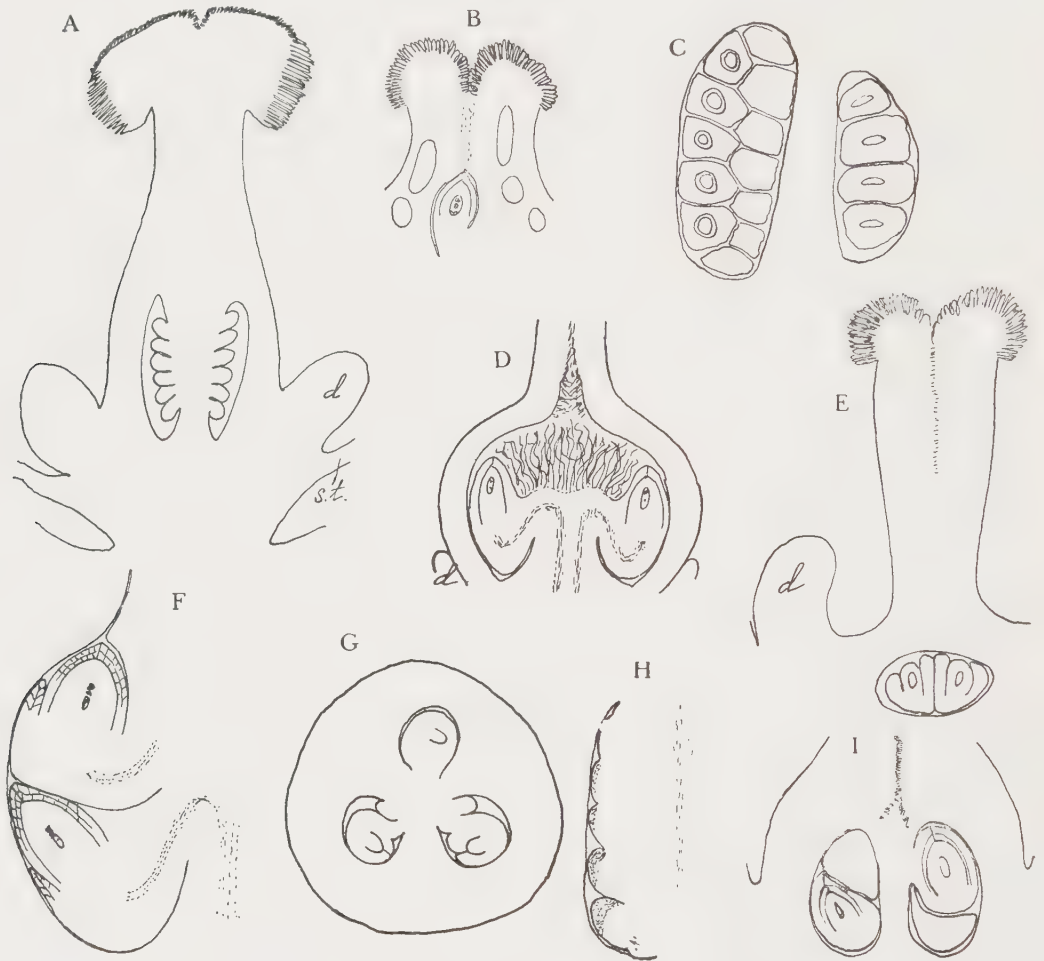


Fig. 18. *A Swietenia Mahagoni*. Gynaecium. *d* disk, *st* staminal tube. $\times 30$. *B Aglaia odoratissima*. Gynaecium. Secretion cavities. $\times 70$. *C Swietenia macrophylla*. Longitudinal section through the ovary chambers. $\times 30$. *D Turraea obtusifolia*. Longitudinal section through the ovary showing the pilosity on the placenta. *d* disk. $\times 30$. *E Walsura pinnata*. Gynaecium. Ovules collateral. *d* disk. $\times 30$. *F Algaia glabriflora*. Longitudinal section through an ovary chamber, showing the ovules at the tetrad division. $\times 185$. *G Dysoxylum alliaceum*. Transverse section through the ovary. $\times 30$. *H Cedrela Glaziovii*. The ovules arise acropetally. $\times 100$. *I Aphanamixis grandifolia*. Longitudinal section through the ovary. $\times 30$.

pointed upwards, as seen in fig. 17 A, 18 F, so that a longitudinal section through the gynaecium gives also the best cuttings through the ovules. Such, however, is by no means the case throughout. A certain heterotropy is not unfrequently met

with. Thus, I have often obtained the best sections from cross-cut ovaries. In these instances, the ovules have consequently, for one thing, not been pendulous, but standing out horizontally from the placenta, and besides, turned round their axes, so that the micropyle has taken an horizontal direction. Fig. 18 G and several more are from cross-cut ovaries. Occasionally, however, the orientation of the ovules was so irregular that it proved extremely difficult to obtain good cuttings, especially of such ovaries as have only two ovules in each chamber. Numerous series of sections were needed in order to make things quite clear and unmistakable. In chambers with many ovules the knife will easily score a point, no matter if the cut is made transversely or longitudinally. In such ovaries the ovules are very irregularly directed in the row. In the middle of the chamber they are, for the most part, pointed horizontally outwards from the placenta, and turned, so that a transverse cutting through the ovary gives good sections of the ovules. On the other hand, those occurring towards the ends of the row are better cut lengthwise. This appears from several figures. The epitropous curve is not seldom more or less uncompleted, so that the ovule becomes hemianatropous. In other genera there are indications of a campylotropous curve of the nucellus, as in *Turraea*. Also wholly atropous ovules occur in the family (*Xylocarpus*), and even apotropous (*Cedrela*). Collateral ovules retain their epitropous, pendulous position (fig. 18 E).

Nucellus. Archesporium. Integument.

Very early, sometimes even before the papilla of the ovule has commenced its epitropous curve, the archesporium becomes visible in the nucellus point, and as usual formed by enlargement of the nucleus and the nucleolus in one or several cells. I have not examined the earliest stage in all the species, but in several instances I have seen a subepidermal archesporium, and I am inclined to the belief that this feature is indeed characteristic of the whole family. In weak nucelli there is only one archesporial cell, which seems quite natural, seeing that nutritional conditions must be supposed to play a certain rôle here as well as elsewhere. In more strongly developed nucelli one often finds that several cells in the nucellus point have assumed an archesporial character.

The development of the ovule, before the tetrad division, takes place in the following way in the different genera.

Cedrela. The 5-roomed ovary in *C. Glaziovii* has in each chamber two rows of apotropous ovules (fig. 17 G), with the funicle sides facing each other, so that the best sections are obtained from cross-cut ovaries (fig. 19 B). In the rather long ovular papilla, the subepidermal archesporium becomes visible at the same time as the commencing curve is distinguishable (fig. 19 A). At the same time the inner integument commences through a periclinal division in the epidermis, starting on the outer side. The archesporium in the ovules here concerned consisted of two cells, evidently formed by an initial cell divided by means of an

antichlinal wall. The ensuing stage, where a parietal cell has been formed, is seen in fig. 19 B. The nucellus is at right angles to the funicle, the inner integument is still somewhat retarded at the inside, the outer one is being formed by periclinal division on the outside of the inner. The archesporial cell has already, under only one parietal cell, entered on the typical synapsis stage that is characteristic of an E. M. C. preparing for heterotypical division. The nucellus is still

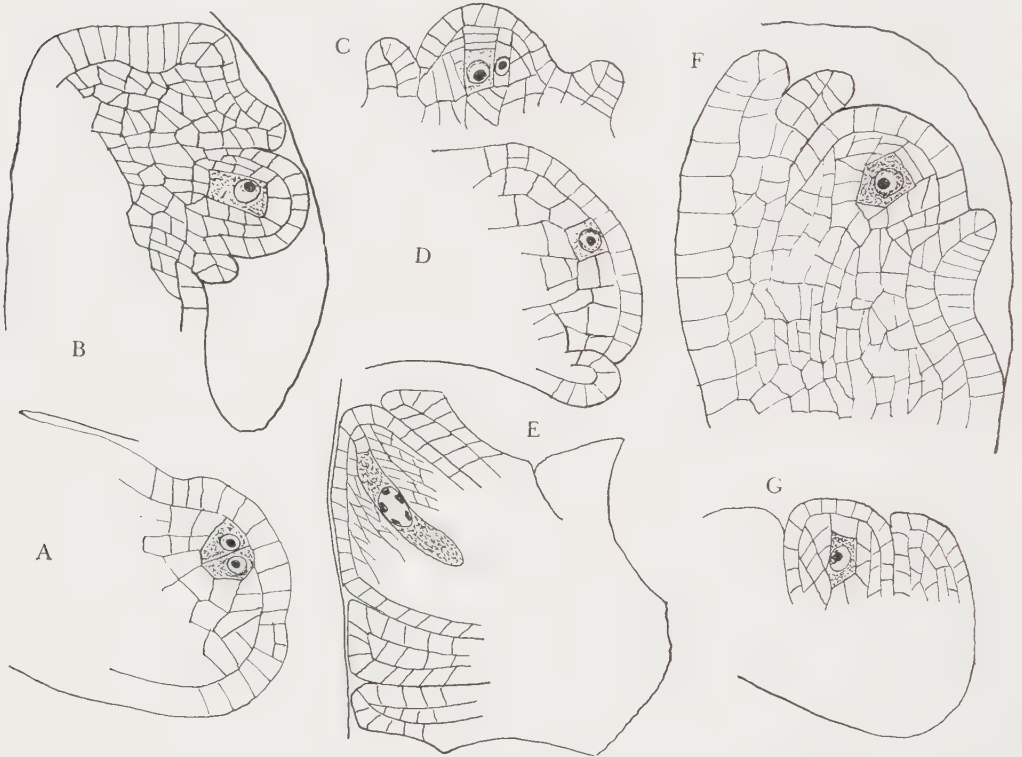


Fig. 19. A-B *Cedrela Glaziovii*. A Two archesporial cells. The integument starts on the one side. $\times 485$. B E. M. C., one tapetal cell. $\times 400$. C *Khaya senegalensis*. E. M. C., three tapetal cells. Accessorial mother cell. $\times 485$. D-E *Chukrasia tabularis*. D Archesporial cell. $\times 485$. E Embryo sac mother cell. Integuments. $\times 400$. F *Swietenia Mahagoni*. E. M. C., two parietal cells. Integuments. $\times 300$. G *Dysoxylum alliaceum*. E. M. C. Unitemic. $\times 300$.

A-B, F-G Transverse sections of the ovaries.

weak; only a couple of cell strata envelop the E. M. C.; the chalazal region is more massive.

Unfortunately, I have not had at my disposal later stages of this species.

The same remark applies to *Khaya senegalensis*; only young material was fit for analysis. This species, too, has a multiovulate placenta, like *Cedrela*, and an archesporium of several cells. Fig. 19 C shows a dominating E. M. C. with three parietal cells, but there were, besides, a number of accessory ones, less advanced. The nucellus is still only slightly developed, the inner integument is growing out,

2-layered. The outer has also been observed, wherefore it is evident that the ovule is crassinucellate, bitegmic. Of this species I have also cut older ovaries. They were almost empty, but nevertheless fully developed. Small, dried-up remnants of ovules remained on the placenta.

Of *Chukrasia tabularis* I have had a somewhat richer material. In the three-roomed ovary (fig. 17 K) there are numerous ovules (fig. 17 L) with rather varying orientation, as shown by the transverse and longitudinal sections. In the still atropous ovule, which is somewhat flattened on account of lack of space, is seen a subepidermal archesporial cell (fig. 19 D). The nucellus is strongly developed, the inner integument more advanced on the one side. As soon as the archesporial cell has given rise to one or two parietal cells, it has already assumed the appearance of an E. M. C. and acquired considerable dimensions. Frequently it then reaches right down into the chalaza (fig. 19 E). The nucleus was in synapsis and contained some rather large chromosomes. The integuments grow rapidly; in the figure they are already on a level with the nucellus. The space is scanty; the ovules become squeezed and angular, the integuments and the nucellus abut against the ovary wall and get flattened. This species has an obturator, as shown by the transverse section (fig. 17 K). The mother cell commences a tetrad division and develops into an E. S. under about 4 parietal cells.

Swietenia. As to *Mahagoni* I can only speak about early stages, as all the older ovules examined by me were empty or containing only withered remnants of ovules and were, besides, destroyed by caterpillars. *Swietenia* has a 5-roomed ovary containing about 10 or 12 ovules in two rows in each room (fig. 18 A). Space and orientation are the same as in the preceding genus. An archesporial cell is developed into an E. M. C. under a few parietal cells (fig. 19 F). The young ovule is thick and massive, as are also the integuments, although they consist of only two layers, to begin with; but the cells are elongated and palisade-like. *Sw. macrophylla* also gave a number of empty ovaries, but many of them were filled with well developed ovules, as shown by fig. 18 C. Of this species I had no earlier stages, only ready built and fecundated embryo sacs. There is no reason, however, for doubting a regular development of the E. M. C. in *Swietenia*. Fig. 27 E shows how, in a later stage, the inner integument has acquired a strong swelling at the point.

On *Carapa guianensis* we have, as has been mentioned before, a statement by Mrs. KRETZKY-DERSCH (communicated by SCHNARF 1931, p. 142), concerning the development of the ovule. She says that the ovule of *Carapa* is crassinucellate, bitegmic; that the chalazal region is strongly developed, and that an archesporial cell gives rise to a parietal cell.

The 4—5-roomed ovary holds about 6—8 ovules in each chamber. In the young ovule, which is rather long and straight and furnished with two outcropping integuments, appears a subepidermal archesporial cell. The nucellus is well developed (fig. 20 A). At the formation of two parietal cells the archesporial cell has assumed the E. M. C. character. The mother cell division takes place, at times,

under only one parietal cell, which stage is shown by fig. 22 B. Also the heterotypical metaphase in fig. 22 A was found under only one parietal cell. The nucellus and the integuments remain feebly developed in *Carapa*, although, as KRETZKY-DERSCH (l. c.) says, the chalazal region is somewhat stronger. The E. S. absorbs the whole of the nucellus, as far as the epidermis (fig. 24 A). The material for *Carapa* was rather bad. The gynaeceums, and also the ovules, were sapless and resinous. The tissues were poor in plasma, or quite empty, except the archesporium and the E. M. C. Most probably such ovules abort in an early stage of the development of the E. S. I have had no later stages at my disposal than 4-nucleate embryo sacs.

For *Xylocarpus*, which is closely related to *Carapa*, I have not had any material. About *X. granatum* (= *Carapa moluccensis*) KARSTEN (1891) states the following: The ovule »beherbergt nur in seinem oberen Teile vier kleine Höhlungen, in welche von der centralen placenta aus je 2—3 Ovular-Anlagen hineinragen. Die ovula sind atrop mit der Mikropyle sehr wenig der Blütenbasis zugeneigt. Sie besitzen zwei Integumente. Über die Entwicklung der ovula bin ich leider nicht im Stande, irgendwelche Angaben zu machen. Das gesammte mitgebrachte Material älterer Knospen und Blüten besass verkümmerte ovula oder war von Insektenlarven seines Fruchtknotens beraubt».

As is the general rule in all of the following genera, biovular rooms occur in the ovary. The ovules are, as a rule, placed above each other; only in a few genera they are collateral.

Turraea forms, in its globular, somewhat flattened ovary, containing five or more chambers (fig. 18 D), 2 basal, collateral ovules. In the young ovular papilla, which is short, thick, and still straight (fig. 20 G), is formed the archesporium, here often consisting of several cells. In fig. 20 G there were, besides a subepidermal cell, a number of others with equally advanced nucleoli. They were frequently found under several strata of cells. Thus, they must either have assumed an archesporial character in the position where they were found; or, they have originally been subepidermal and since then retained their archesporial shape. The latter opinion as to the origin of the archesporium in higher plants is the commonly accepted one. But from this it is evident that parietal cells must be regarded as potential archesporial cells. There are often several archesporial cells in one and the same row. Most probably, however, the inner cells in fig. 20 G have assumed their archesporial shape where they lie. Fig. 20 E shows a later stage with two definitive tapetal cells. In this nucellus there were found also some other advanced cells. The ovule is now bent upwards. Only one cell has been observed to pass through heterotypical division. In *Turraea* the nucellus is, from the very first, rather strong, which perhaps explains, partly, the several-celled archesporium. The E. M. C. also very soon acquires considerable dimensions (fig. 20 H). Sometimes a parietal cell advances as well (fig. 20 H-I). The reduction division takes place under 4 parietal cells, as shown by fig. 20 I. At the appearance of the archesporium, the integuments are not yet visible (fig. 20 G), but arise later

on in the usual way. The outer integument is in *Turraea* originally weak, 2-layered (fig. 20 I), but subsequently grows one layer thicker. The micropyle is formed by the inner integument. In *Turraea* the epidermis of the inner integument grows palisade-like, in later stages; only, however, round the micropyle. Thus no real tapetum exists. Round the nucellus the integument cells are not tapetum-shaped. The position of the ovules is, in later stages, different in *obtusifolia* and *floribunda*.

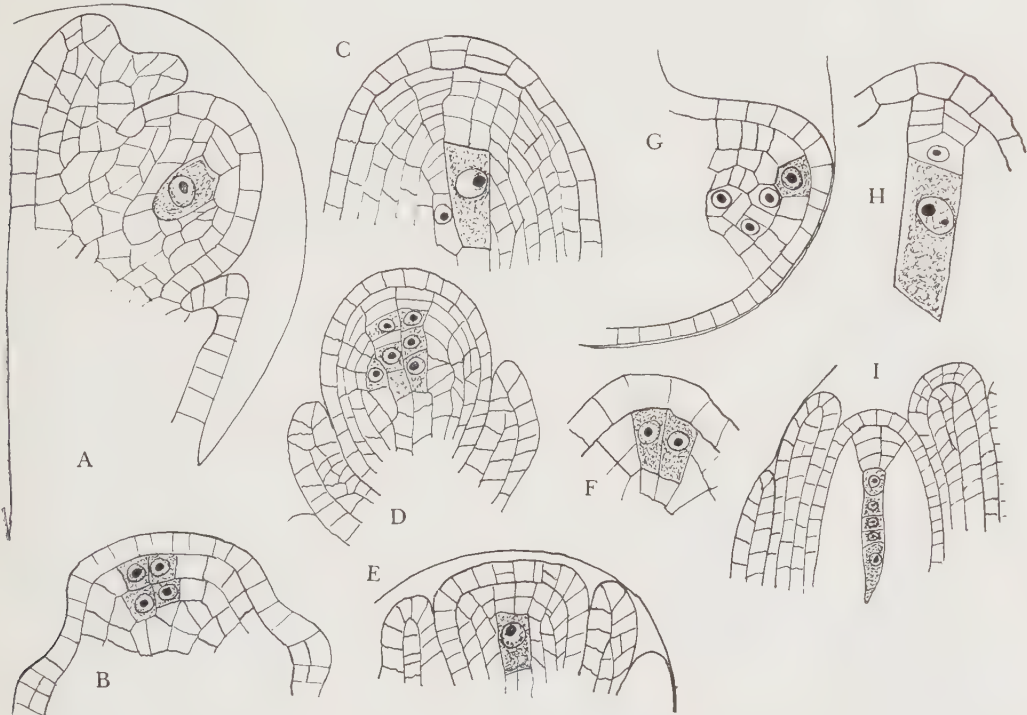


Fig. 20. *A* *Carapa guianensis*. Embryo sac mother cell. Two tapetal cells. Integuments. The ovary cross-cut. $\times 485$. *B-C* *Melia Azedarach*. *B* Many-celled archesporium. Commencement of the inner integument. $\times 485$. *C* Accessorial E. M. C. in the same nucellus as in fig. 23 *B*. Periclinal division in the epidermis. $\times 485$. *D* *Melia Candollei*. Many-celled archesporium. $\times 300$. *F* *Dysoxylum nutans*. Two archesporial cells. $\times 485$. *G, E, H-I* *Turraea obtusifolia*. *G* Archesporium. $\times 485$. *E, H* Embryo sac mother cells. *E* $\times 485$, *H* $\times 600$. *I* Tetrad. One tapetal cell advanced. Integuments. $\times 300$.

In the former the collateral position persists, see fig. 18 D. The 10 ovules are on a level, on top of a column, two by two, and separated by the five walls of the ovary. Above the pillar, the rooms communicate. The placenta, in *obtusifolia* as well as in *floribunda*, is covered with a long pilosity, as in fig. 18 D, 26 G. The stylar canal, too, is hairy. The placentation in *Turraea obtusifolia* greatly reminds of that in *Simmondsia californica* (see above, p. 9). Strong vascular strands run into the basal part of the ovary and branch off to the ovules. Early enough one can discover in the *Turraea* species a campylotropous curve, which later on becomes

more accentuated. A hypostasis of small resinous cells is then formed in the chalaza. In *T. floribunda* the ovules do not remain collateral, but get shoved over one another, as is usually the case in 2-ovulate rooms.

Melia. The ovary is 5-celled, containing in each cell two ovules, placed a little above each other, the lower pendent, the upper more or less turned upwards (fig. 17 A). In the slightly bent ovule the archesporium and integuments begin to grow out (fig. 20 B). The nucellus is strongly developed, and there occurs, already in the subepidermal stage, a many-celled archesporium, at least in most cases. Ovules such as in fig. 20 D with the whole interior of the nucellus occupied by well-developed archesporial cells I have often observed in the material of *Melia Azedarach* and *Candollei*. As to *M. floribunda* I have not investigated this species in so early stages, but it does not deviate in other respects from the other two. As a rule one E. M. C. passes through the reduction division; often, however, there are, besides, one or more accessorial embryo sac mother cells. Fig. 20 C and 23 B are from two consecutive sections of *Melia Azedarach*, the one with a tetrad, the other with a large and well-developed E. M. C. together with a smaller one. And in *Azedarach* as well as in *Candollei* I have in several cases seen two fully developed tetrads in one and the same nucellus, as shown in fig. 22 G. The number of parietal cells is 4—6, besides the nucellus cap, which has two or three strata. Strong vascular strands descend into the funicle to the well-developed chalazal region (fig. 17 A). At first the integuments in *Melia* grow very slowly, especially the outer one (fig. 20 D). At the tetrad division they rise parallel to the nucellus point and are then of the same length and thickness, and 3-layered. Later on they become strongly swelled at the point, as fig. 27 D shows.

Sandoricum has small collateral ovules. During the development of the E. M. C. the nucellus is solid (fig. 21 C); the mother cell generally divides under six or seven parietal cells, and besides these we have, as in most of the *Meliaceae*, a cap of a few layers.

During the formation of the E. S. the nucellus is absorbed, in *Sandoricum*, so that only one or two cell strata remain under the epidermis. The inner integument grows beforehand up to the nucellus point and is, as usual, 3-layered. Later on also the outer grows up to the point. This is 2-layered.

Dysoxylum. Of this genus, the second in the family as regards numbers, containing about a hundred species, I have investigated nine. Great conformity prevails within the genus. The ovary has 3, or more seldom 4, cells (fig. 18 G). It contains two ovules in each chamber, placed above each other, in *ramiflorum* more or less collateral. They turn and grow horizontally out from the placenta, so that good sections are obtained from cross-cut ovaries (fig. 19 G). The subepidermal archesporium does not arise until the epitropous curve is fairly advanced. In fig. 19 G the nucellus is already at right angles to the funicle, although only one parietal cell has as yet been formed. Fig. 20 F shows, in *nutans*, two subepidermal archesporial cells, and fig. 21 A a somewhat later stage in the same species, with a group of cells equally advanced under two parietal cells. The integument

is still only visible in the nucellus epidermis. In fig. 21 D there is only one E. M. C. under three strata. Several archesporial cells were observed also in other species of this genus, e. g. in *ramiflorum*, and *alliaceum*. In the last-mentioned species

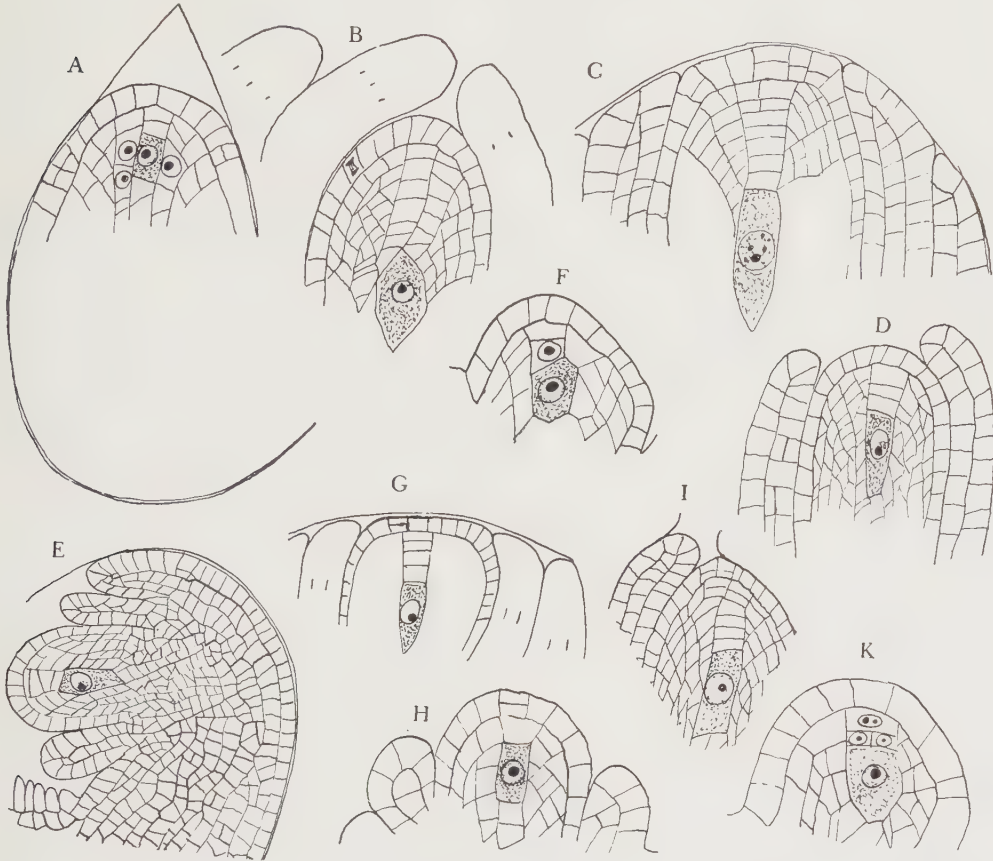


Fig. 21. A, *D* *Dysoxylum nutans*. A Many-celled archesporium. Commencement of integument. $\times 400$. D Embryo sac mother cell. $\times 400$. B *Dys. macrothyrsus*. E. M. C. Integuments. $\times 300$. C *Sandoricum Koetjape*. E. M. C. 7 tapetal cells. Integuments. $\times 485$. E *Aglaia argentea*. E. M. C. Integuments. $\times 300$. F-G *Walsura pinnata*. F Two archesporial cells. $\times 485$. G E. M. C. 4 tapetal cells. Integuments. $\times 300$. H *Aglaia rufa*. E. M. C. $\times 485$. I *Dysoxylum ramiflorum*. E. M. C. Parietal cells. $\times 300$. K *Chisocheton divergens*. E. M. C. $\times 485$.

the nucellus often had the same appearance as has been stated above as to *Melia* (fig. 20 D), i e., the whole of its interior consisted of about 20 typical archesporial cells, among which, generally, only one predominated. Exceptionally, I have seen that more than one mother cell has divided and developed further, as in *Dysoxylum nutans*, fig. 25 D, where two embryo sacs existed in one and the same nucellus, or in *D. alliaceum*, which had, as in fig. 23 E, two tetrads in one nucellus.

The number of parietal cells is somewhat variable. In fig. 19 G the E. M. C. has already gone into synapsis under one parietal cell. In some other cases I have observed, in the same species, that the mother cell divides under two parietal cells. At times, however, the division of the mother cell is somewhat retarded, so that several parietal cells have managed to come into existence. For example, I have seen, in *D. aliaceum*, several cases of diakinesis under three parietal cells. The tetrads in fig. 23 E and 22 P were found under four strata. In *D. macrothyrsium* and *ramiflorum* the mother cell migrates further down into the nucellus, before it divides, as is shown by fig. 21 B and I. In *Dysoxylum* the nucellus is well developed.

The integuments are in this genus somewhat different. The inner one arises at the same time as the archesporium, fig. 21 A. In *alliaceum* only one integument exists (fig. 19 G); this is then, however, as thick as the two in other species. The *Dysoxylum* are otherwise bitegmic. In most of the species the micropyle closes at the tetrad division. A somewhat thicker inner integument is formed in *macrothyrsium* (fig. 21 B), whilst *ramiflorum* has a weak inner but a strongly developed outer integument as shown by fig. 22 L. At the tetrad division the outer integument here forms the micropyle, whereas the inner is almost rudimentary, and two-layered. Later on also this integument grows up over the nucellus point.

Chisocheton has small flowers and ovaries with often only one ovule in each cell. On account of the narrow space this single ovule is often somewhat differently directed. Often I have found that, at the time of the development of the E. S., the micropyle is directed downwards. The nucellus is comparatively weak. Fig. 21 K shows, in a small ovular papilla, an E. M. C. under two parietal cells in *Ch. divergens*. The material of this genus has been resinous, sapless and bad. The genus is bitegmic. The inner integument is 4-layered, and, accordingly, by one stratum thicker than is generally the case in this family. The outer is shorter and weaker at the time of the formation of the E. S.

As to *Aphanamixis* I have not seen the archesporium. A 3-celled ovary has in each chamber two ovules (fig. 18 I). The nucellus is rather solid. The E. S. is formed under about 4 cell strata. The genus is bitegmic. A sometimes slightly curved micropyle is formed by both the integuments, the inner of which is swelled at the point, especially on the inner side (fig. 23 I).

The genus *Aglaia*, about 70 species strong, has, as a rule, very small flowers and ovaries. »Fruchtknoten sehr klein, 1—2-fächerig, selten 3-fächerig, in jedem Fache 1—2 Samenanlagen» (HARMS 1896). I have also met with a 4-celled species, namely *A. Eusideroxylon*. My material comprises 12 species. The infinitesimal size of the ovaries in this genus, and also the resin in the tissues, has naturally made it no easy task to study the embryology of these plants. About the smallness of the ovule one will get a notion from the following statement. The ovule designed in fig. 18 B of *A. odoratissima* was divided into 8 sections of 10 microns each, i. e., this ovule had a thickness of about 8/100 mm., when the E. S. was

ready-formed. A similar measuring of *A. odorata* gave double that size, and this species has not an especially large ovary. See further the figures.

The pollen grains in these plants are very small (see fig. 30), and also the cells and the nuclei. A nucellus such as in fig. 25 B gives the impression of being quite normal in structure.

Such small-flowered species as *A. odoratissima*, and others, have only one ovule in each room. Several species have two. Some of them, as e. g. *A. Eusideroxylon*, have rather large flowers, ovaries and ovules.

An archesporial cell arises subepidermally and migrates into the nucellus under, as a rule, only a few parietal cells, before developing further. Fig. 21 E, H show E. M. cells in *A. argentea* and *rufa*. *A. odorata* has a remarkable cap formation in the nucellus point (fig. 23 C).

Aglaia is, as are also other genera, bitegmic. *A. odorata* has, on account of the strong cap, a rather weak inner integument. This is otherwise normally developed (fig. 21 E), and forms the micropyle. It is, as usual, 3-layered, except in the very small-flowered species, which often have a 2-layered inner integument (fig. 18 F, 25 B). Also the outer integument in these species is weak and retarded, and has 2 strata (fig. 18 F). As to *A. eleagnoides* the material was very unsatisfactory. The ovules were, already in early stages, abortive.

Finally we have *Walsura*, which has 2 collateral ovules in each chamber (fig. 18 E). The nucellus is well developed. One, or at times, several archesporial cells developed into E. M. C. under four to six strata of tapetal cells (fig. 21 G), before the tetrad division began. In fig. 21 F there is an indication of a many-celled archesporium by enlargement of the nucleus and the nucleolus in a parietal cell. The integuments are normal, and at the tetrad division equally developed (fig. 21 G).

Cap formation by means of periclinal division in the nucellus point is frequent in the *Meliaceae*, as is shown by the figures mentioned above. The strata are, as a rule, only few, but in certain cases the cap is rather thick, as in *Dysoxylum ramiflorum* (fig. 22 L), or still more in *Aglaia odorata* (fig. 23 C), where the tetrad was found under about 20 strata, many of which are no doubt cap cells. Many of the small *Aglaia* seem to lack the cap. I have, however, seen it in *odoratissima*, *rufa*, and *eximia*.

As a summing up of the above statements concerning the nucellus, archesporium, and integuments in this family the following may be said: the *Meliaceae* have crassinucellate, bitegmic ovules; certain genera, as *Turraea*, *Melia*, and *Dysoxylum* have a rather massive nucellus and, as a rule, a many-celled archesporium. Many genera have small ovaries and ovules and, accordingly, a rather weak nucellus and only one archesporial cell. The E. M. C. divides under a different number of parietal cells. There is only one integument in *Dysoxylum alliaceum*. The outer integument is often represented on the raphe-side by a more or less high border. This integument often grows somewhat slowly and does

not reach the nucellus point until in later stages. The inner integument is, as a rule, 3-layered, at the point sometimes swelled, as in *Swietenia*, *Melia*, etc. No integument tapetum is formed in this family.

The tetrad division. The formation of the embryo sac.

As regards the division of the megaspore mother cell and its further development into an embryo sac, great conformity prevails throughout the family of *Meliaceae*. No irregularities of any importance are met with in the different genera. In this respect the family seems very homogeneous. A series of figures will show the division of the E. M. C. Having seen typical embryo sac mother cells in such prophase stages as e. g. synapsis and diakinesis, in the majority of the species investigated, I have no doubt but that in this family the mother cell passes through chromosome reduction.

The tetrad division. Excepting *Cedrela*, *Swietenia*, *Khaya*, and *Chisocheton*, in which tetrad division was not included in the material used, I have, in all the other genera, and, with few exceptions, in all the species, observed either the division of the mother cell, or completed tetrad cells, or remains of them, from which I have been able to conclude that the division takes place according to the normal type, with wall formation after the heterotypical as well as after the homotypical division.

Heterotypical spindles have been observed in *Carapa guianensis* (fig. 22 A), *Dysoxylum macrothyrsus* and *ramiflorum* (fig. 22 C, E). They have been found in the centre of the cell. The chromosomes seem to be small and numerous. I have not made a point of searching for their number. In the pollen mother cell of *Walsura pinnata* I have seen about 13 gemini (fig. 29 E). As has been mentioned before, a wall is at once formed, so that two dyad cells arise. Such dyad cells have been seen e. g. in *Carapa* (fig. 22 B), *Turraea obtusifolia* (fig. 22 H), *Melia Candollei* (fig. 22 F), and *Dysoxylum nutans* (fig. 22 D). In *Carapa* the micropylar cell predominated, so that one might possibly assume that it had a tendency towards developing into an E. S. My material has not been sufficiently decisive, but the dyad and other observations seem to point in this direction. In *Melia Candollei*, too, the upper dyad cell had at least the same size as the lower, but in this species I have had a clear instance of an E. S. formed by the chalazal macrospore. In *Turraea* the lower dyad cell predominated, in *Dysoxylum nutans* the cells were the same size.

The homotypic division was seen in *Turraea obtusifolia* (fig. 22 H). The spindles lay lengthwise but somewhat obliquely, in the lower cell a little above the middle, wherefore division would probably have resulted in a somewhat larger size for the nethermost tetrad cell.

Tetrad cells or traces of them have been observed in a large number of species of which the following may be mentioned.

In *Turraea obtusifolia* (fig. 20 I, 22 I) was observed, besides a fine tetrad, also a parietal cell as accessory E. M. C. In the *Melia* species, two tetrads in the same nucellus were observed several times; likewise more than once, besides a tetrad, one or two embryo sac mother cells in the same nucellus, as shown by fig. 20 C and 23 B, which are from consecutive sections.

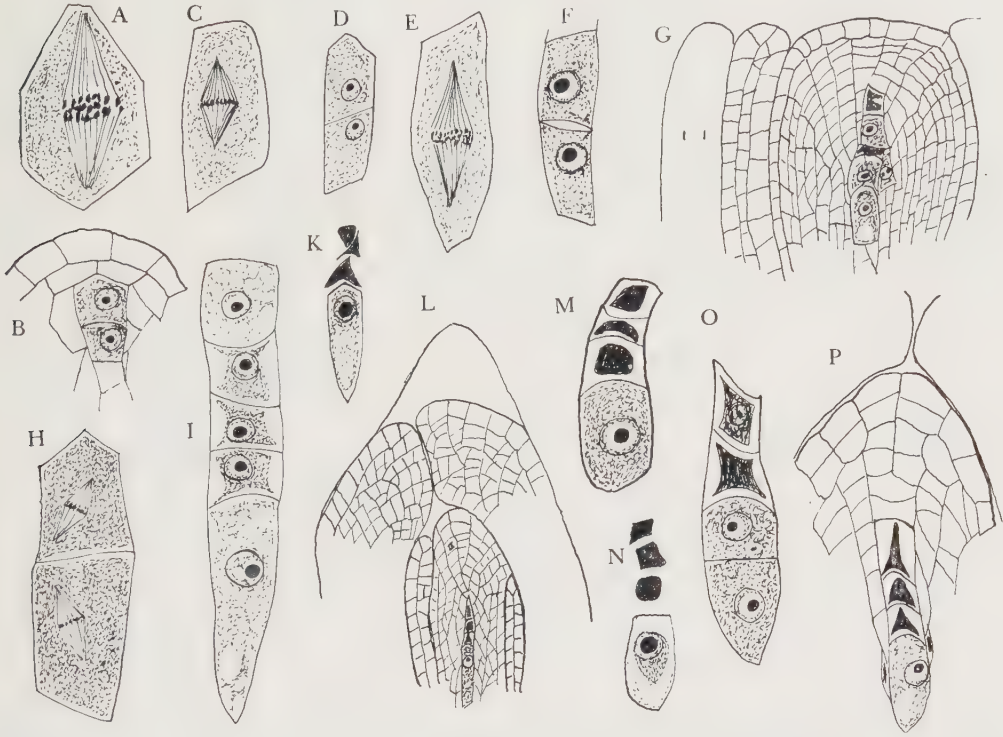


Fig. 22. A-B *Carapa guianensis*. A Heterotypic spindle. $\times 1800$. B Dyad. $\times 600$. C *Dysoxylum macrothyrsum*. Heterotypic spindle. $\times 485$. D *Dys. nutans*. Dyad. $\times 485$. E, L *Dys. ramiflorum*. E Heterotypic spindle. $\times 900$. L 1-nucleate embryo sac and tetrad remnants. Integuments. $\times 185$. F-G *Melia Candollei*. F Dyad. $\times 900$. G Two tetrads. $\times 400$. H-I *Turraea obtusifolia*. H Homotypic division. $\times 1030$. I Tetrad. Accessorial E. M. C. (=fig. 20 I). $\times 1030$. K *Aglaia glabriflora*. Primary 1-nucleate embryo sac. Tetrad remnants. $\times 600$. M *Dysoxylum amooroides*. Primary E. S. with tetrad remnants. $\times 900$. N *Aglaia Ganggo*. Ditto. $\times 830$. O *Sandoricum borneense*. Two tetrad cells advanced. $\times 900$. P *Dysoxylum urens*. 1-nucleate E. S. with tetrad remnants. $\times 485$.

In most of the *Dysoxylum* I have remarked tetrads, in some instances two in the same ovule. The following particulars may here be given. Fig. 22 P shows a typical tetrad in *D. urens*, seen several times; fig. 22 M another, in *D. amooroides*. Fig. 23 E has two 2-nucleate embryo sacs, arisen from the chalazal megaspores in two tetrads in the same nucellus of *D. alliaceum*. Necrotized remains of the upper sister cells are visible. The uppermost sister cell in one of the tetrads was, however, still vital. Fig. 23 H gives a tetrad of *D. ramiflorum*, etc.

Some tetrads of *Aglaia* may also be mentioned. Fig. 22 K is a 1-nucleate and fig. 25 B a 4-nucleate E. S. with dying-off upper sister cells in *A. glabriflora*, fig. 23 C a 1-nucleate E. S. with tetrad remnants in *odorata*. *Ganggo* and *odoratisima* have also yielded similar figures.

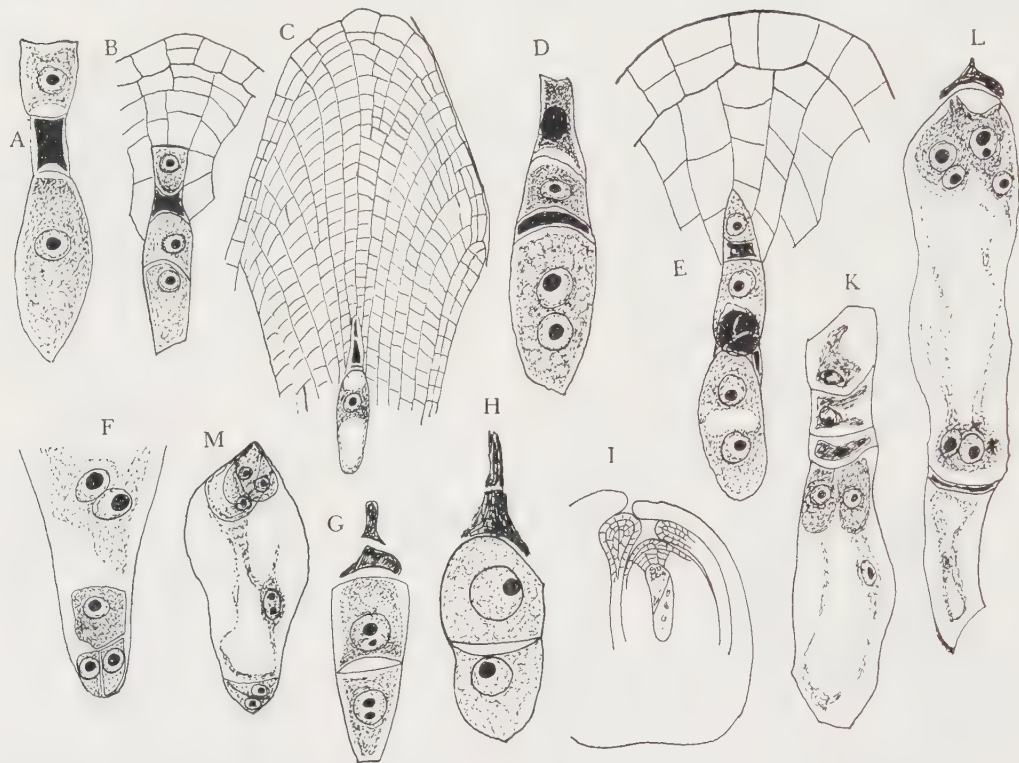


Fig. 23. A *Melia Candollei*. 1-nucleate embryo sac. The uppermost tetrad cell advanced. $\times 830$. B *Melia Azedarach*. Tetrad in the same nucellus as fig. 20 C. C *Aglaia odorata*. Primary 1-nucleate E. S. and tetrad remnants. Strong nucellus cap. $\times 300$. D-E *Dysoxylum alliaceum*. D 2-nucleate E. S. No vacuolization. One upper tetrad cell vital. $\times 900$. E Two 2-nucleate embryo sacs in the same nucellus. $\times 485$. F *Melia Azedarach*. Two antipodals at the point of the sac. Polar nuclei. $\times 900$. G *Walsura pinnata*. Two megaspores developed. $\times 900$. H *Dysoxylum ramiflorum*. As the former. $\times 900$. I, L *Aphanamixis grandifolia*. I Two embryo sacs. Integuments. $\times 85$. L 8-nucleate E. S. of the next uppermost megaspore. $\times 600$. K *Chukrasia tabularis*. E. S. and tetrad remnants. $\times 900$. M *Aglaia eximia*. E. S. Primary endosperm nucleus. $\times 485$.

Sandoricum has likewise a normal tetrad division (fig. 22 O) and the same remark applies to *Walsura* (fig. 23 G).

The row tetrad is the only one that has been observed.

The megaspore development. As a rule the chalazal megaspore develops into an E. S., and the upper sister cells degenerate and get absorbed. In many species I have, however, observed that the upper sister cells have grown, more or less, and even that one of them has developed into an E. S. The following should be specially noticed as regards the megaspore germination.

As a rule, *Chukrasia*, and *Turraea* form an E. S. out of the chalazal megaspore (fig. 23 K, 22 I). As has been mentioned above, there are tendencies, especially in *Melia*, towards the development of several embryo sac mother cells in the same nucellus. This statement is also applicable to the megaspores. Fig. 22 G shows examples of two tetrads in the same nucellus with tendencies towards further growth in both of the lower cells in each tetrad. Fig. 23 A-B are tetrads of the same genus with a tendency towards development in more than one megaspore. In spite of my having observed several such tetrads in *Melia*, it may be safely presumed that, as a general rule, the chalazal cell becomes the E. S., a thing I have actually observed in a number of cases, see for instance fig. 24 C, 25 F.

Sandoricum has shown a similar megaspore development. In fig. 22 O, for instance, both the chalazal cells are proceeding towards E. S. formation. In the copious genus *Dysoxylum* the same variations are met with as in the other genera. Fig. 23 E has already been spoken of. Fig. 23 D is from another nucellus, in which every second tetrad cell showed vitality. Such nucelli have almost been the rule in *D. alliaceum*. *D. ramiflorum* is represented by fig. 23 H, in which the nethermost cell but one predominates; most likely it would have developed into an E. S. In other instances this species has given evidence of normal megaspore development. *D. urens*, *amooroides*, and *Blumei*, have shown both normal tetrads and abnormal ones, like those found in *alliaceum* and other species. In one instance *D. nutans* has been observed with two fully developed embryo sacs in the same nucellus, as appearing in fig. 25 D a-b, which are from consecutive cuttings. As, on account of their position, these sacs cannot very well be regarded as arisen from one and the same tetrad, it must be inferred that in this ovule two embryo sac mother cells have gone through the whole process of development into ready built embryo sacs.

In *Aglaia* only the normal megaspore development has been observed. I have inserted figures of *glabriflora*, *Ganggo*, and *odorata* (22 K, N, 23 C).

In *Aphanamixis* I have seen many cases of the regular megaspore development, but also several deviations. Thus, fig. 23 L shows that the uppermost tetrad cell but one has predominated and developed into an 8-nucleate E. S., although the chalazal cell has also had certain tendencies towards further growth. Another irregular case is seen in fig. 26 a-b, which are from consecutive sections. Two embryo sacs are visible, and even if their positions do not exclude an origin from one tetrad, it seems more probable that two embryo sac mother cells have been in play here. I have seen several such nucelli in this species, and also instances of the micropylar megaspore having built up an E. S.

Walsura pinnata has shown the same conditions as several others, viz. that both the lower tetrad cells have been advanced (fig. 23 G). *W. quadrilocularis*, on the other hand, has only had normal or chalazal macrospore development.

Carapa guianensis has, according to SCHNARFF (1931), a normal E. S. development.

The formation of the embryo sac. The advancing megaspore mother cell grows

and develops into a 1-nucleate primary E. S. Such have been seen in many species and are here shown in several figures. The nucleus is placed in the middle or upper part of the cell, and this varies as to vacuolization. Having ceased growing, the primary embryo sac nucleus divides, and the daughter nuclei migrate to each pole of the sac, with a vacuole occupying the middle part, as is generally

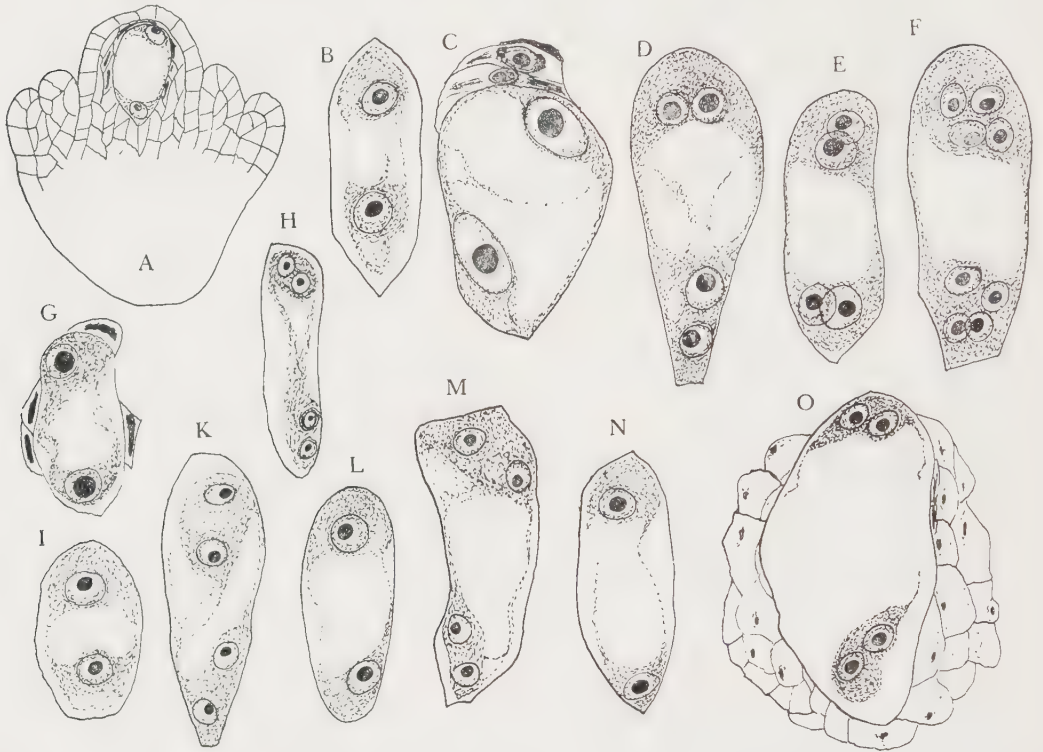


Fig. 24. A *Carapa guianensis*. 2-nucleate E. S. $\times 300$. B *Walsura pinnata*. 2-nucleate E. S. $\times 900$. C-D *Melia Azedarach*. 2-nucleate and 4-nucleate embryo sacs. $\times 830$. E-F *Dysoxylum caulostachyum*. 4-nucleate and 8-nucleate embryo sacs. $\times 600$. G *Aglaia Ganggo*. 2-nucleate E. S. $\times 830$. H *Chukrasia tabularis*. 4-nucleate E. S. $\times 600$. I-K *Dysoxylum urens*. 2-nucleate E. S. $\times 900$; 4-nucleate E. S. $\times 485$. L *Dys. nutans*. 2-nucleate E. S. $\times 830$. M *Dys. ramiflorum*. 4-nucleate E. S. $\times 400$. N *Sandoricum borneense*. 2-nucleate E. S. $\times 1030$. O *Sandor. Koetjape*. 4-nucleate E. S. $\times 830$.

the case. Such normal 2-nucleate embryo sacs have been reported in a large number of species, but only a few have been drawn, as no deviations from the normal type worth mentioning have occurred. The following have been drawn; viz. *Carapa guianensis* (fig. 24 A), *Walsura pinnata* (fig. 24 B), *Melia Azedarach* (fig. 24 C), *Aglaia Ganggo* (fig. 24 G), *Dysoxylum urens*, *nutans* and *alliaceum* (fig. 24 I, L, 23 D-E), and *Sandoricum borneense* (fig. 24 N). All these were normally vacuolized, except *Dysoxylum alliaceum*, whose central vacuole was lacking in fig. 23 D.

The two nuclei divide again, the sac still growing, and with the vacuolization and polarity retained. Normal 4-nuclear embryo sacs are the result of this division. The position of the nuclei at the poles of the sac is, as usual, on account of the space, somewhat different. As a rule they lie abreast in the wide upper extremity of the sac, but in a row above each other at the narrower chalazal pole. Sometimes they lie in a row in both extremities, as in fig. 24 K of *Dysoxylum urens*, sometimes in a row in the upper, and abreast in the lower pole, as in *D. caulostachyum*, fig. 24 E. Fine 4-nucleate embryo sacs have been observed in some 20 species. They have not shown any remarkable structure. Only a few have been drawn; see the figures 24 and 25 B.

Finally, after further growth of the E. S. and with retained vacuolization, a last division takes place. The result of this is an 8-nuclear embryo sac with two 4-nucleate groups, one at each end of the sac. As to the growth of the sac during these divisions, see the figures 24 E-F, and others. Generally it seems to increase to double its volume or more.

The divisions seem to be synchronous in the different parts of the embryo sac. In spite of all my efforts I have found no instance in this family of any asynchronism worth mentioning in the nucleus division.

Undifferentiated 8-nucleate embryo sacs have been seen in several species, e. g. in *Dysoxylum caulostachyum* (fig. 24 F), *Melia Azedarach*, *Aglaia glabriflora* (fig. 25 A), *Aphanamixis grandifolia* (fig. 23 L). I have not been able to follow *Carapa guianensis* any further than to the 4-nucleate stage, but according to SCHNARF (1931) it develops a normal embryo sac with »unbedeutende Antipoden».

Cell formation soon takes place in the embryo sac, and this too seems to be synchronous. The result is an egg apparatus of two synergids and one egg cell in the upper and three antipodals in the lower part of the embryo sac, besides two free polar nuclei which ordinarily meet in the middle part of the sac. Mature younger or older embryo sacs have been seen in most of the species, or more than thirty.

The following is worthy of attention.

In *Chukrasia tabularis* the mature sacs have been in degeneration and more or less hypertrophied. The nucellus has been absorbed to the very end of the point and down into the chalaza. I have even seen the embryo sac pushing out through the point. The polar nuclei have not been observed in fusion; the antipodals become early absorbed.

Melia has had fine embryo sacs such as in fig. 25 F. The nucleoli were exceptionally large. Already in the 2-nuclear E. S. in fig. 24 C they were as large as 4–5 μ . In the mature sac in fig. 25 F they were about the same size in egg-apparatus and polar nuclei. This E. S. may, by the way, be mentioned as an example of an ideal section, because all of the eight nuclei were hit at one time in a cut of 10 μ . The egg-apparatus was in this sac only partly developed. Vacuolization had not yet taken place, the cells were plasma-filled and the nuclei did not occupy their normal positions. Also the cellulose walls were indistinct.

The grouping of the antipodals may be observed. The polar nuclei are in contact in the middle part of the sac.

Sandoricum Koetjape, fig. 25 G, showed a normal egg cell but the synergids of the sac, drawn in the figure, were not quite normal in appearance. The point

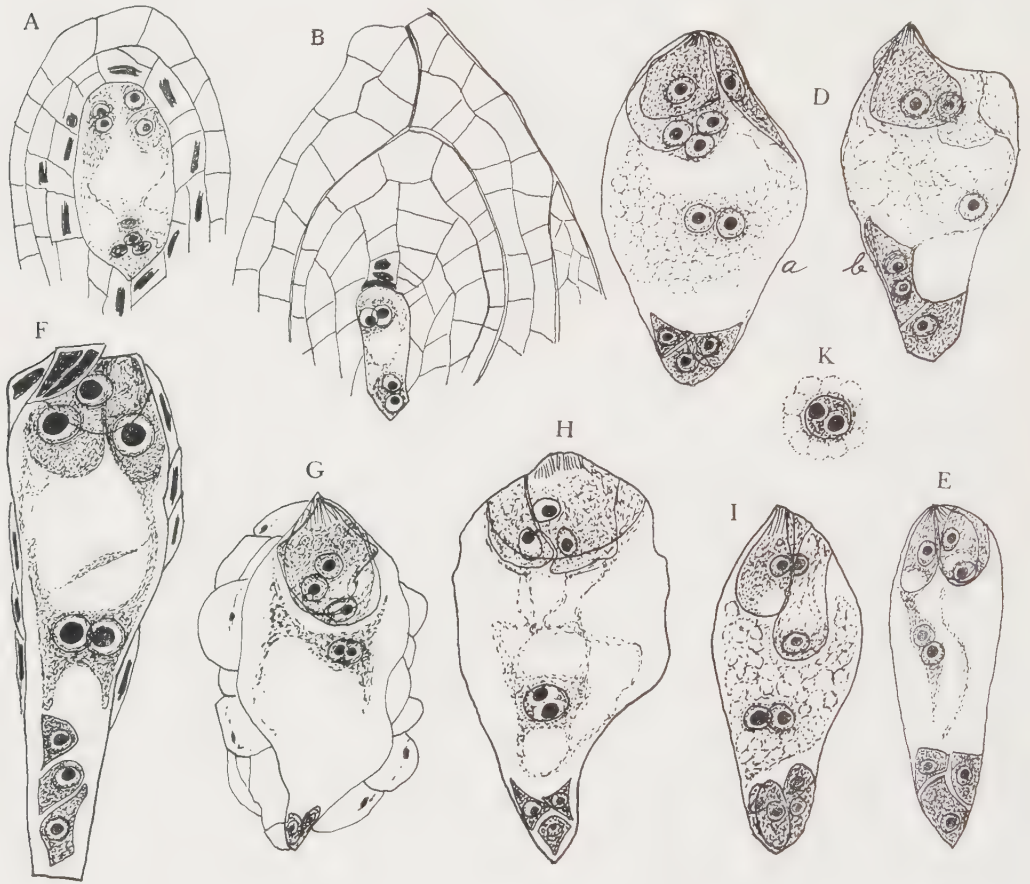


Fig. 25. *A-B Aglaia glabriflora*. *A* 8-nucleate E. S. Nucellus getting absorbed. $\times 600$. *B* 4-nucleate E. S. Tetrad remnants. Integuments. $\times 600$. *D-E Dysoxylum nutans*. *D a-b* Two embryo sacs. Two consecutive sections. $\times 485$. *E* Normal E. S. $\times 485$. *F Melia Azedarach*. Embryo sac. $\times 900$. *G Sandoricum Koetjape*. Embryo sac. Primary endosperm nucleus. $\times 400$. *H Dysoxylum alliaceum*. Embryo sac. Primary endosperm nucleus. $\times 485$. *I-K Chisocheton amboinensis*. *I* E. S. The antipodals more than three. $\times 400$. *K* Primary endosperm nucleus. $\times 600$.

structure was distinct; the polar nuclei had joined. The antipodals were in absorption.

Also the *Dysoxylum* species had normal egg cells, but more or less abnormal synergids. Fig. 26 F is a section through a sac of *D. urens*, containing two long, narrow, plasmous, not fully normal synergids with fine point structure. The egg

cell was normal and lay in another section. The antipodals were insignificant. *D. alliaceum* has had normal egg cells, but I have hardly seen in it any quite normal synergids. In fig. 25 H a certain degeneration seems to have begun in the egg apparatus. Point structure was visible. The polar nuclei had fused, the antipodals were vital. Fig. 25 E is from *D. nutans*. In this sac the synergids too were normally vacuolized. Point structure is visible. Fig. 25 D *a-b* are two consecutive sections of the same species, showing two embryo sacs in one and the same nucellus. Here two embryo sac mother cells have probably been at work, each resulting in a fully developed E. S. They can scarcely have arisen from one and the same tetrad. The antipodals are normal, and the polar nuclei show in the one sac contact, whereas in the other they do not seem to have encountered. The egg cells are more or less normal, but the synergids have, on account of the limited space, a more or less abnormal structure. Point apparatus is visible in both of the embryo sacs.

Fig. 25 I is a quite normal E. S. in *Chisocheton amboinensis*. A striking feature is the lateral insertion of the egg cell below the point of the sac and also its sack-like shape with the nucleus in the bottom far below the synergids. The latter were here normally vacuolized. The antipodals were vital and had even multiplied, which has seldom been noted in this family.

Aglaia rufa and *Eusideroxylon* had excellent embryo sacs with all features well accentuated. The former had often such sacs as in fig. 26 D, i. e. with the synergids vacuolized at the top and the nuclei embedded in plasma in the lower part of the cell. The egg cells were normal, the antipodals, however, in this species rather ephemeral. *A. Eusideroxylon* had exceptionally wide embryo sacs such as in figure 26 C. The antipodals were in this species more vital. The egg cell had the normal appearance. The synergids had the whole top occupied by a strongly green-coloured and, so far as I could find, fibrous substance, whether »Fadenapparat» or »Synergidenkappe» (SCHNARF 1929, p. 139), matters little. The cells were almost plasma-filled with the exception of a basal vacuole. The nuclei lay in plasma in the lower part, as the figure shows. Almost all the embryo sacs I have seen in this species had the same appearance. Two large polar nuclei always lay in contact in the middle or upper part of the sac. Some nucellar cells entered the lower part of the sac shown in fig. 26 C. I cannot decide whether they would develop into embryos, even if this seems probable. For the rest, I saw in this species several embryo sacs of this type. Fig. 23 M is an E. S. of *A. eximia*.

The above-mentioned consecutive sections of *Aphanamixis grandifolia*, fig. 26 A *a-b*, contained two embryo sacs, one of which was shorter. They have probably arisen from two E. M. cells. The different elements were somewhat heterogeneously spread in these sacs; the antipodals in the smaller sac, however, lay quite normally.

Also an E. S. of *Walsura pinnata* is designed, fig. 26 B. The egg cells was normal, but not the synergids, which were supplied with point structure and had

their nuclei in the lower part, as in many of the synergids mentioned above. The antipodals were vital.

As a summing up about the egg apparatus it may be said that the egg cells were normal, the synergids more or less abnormal. In most of the embryo sacs the synergid nuclei were placed in the lower part of the cells, whilst the top was occupied by a »Fadenapparat«. Only seldom was their vacuolization normal. The abnormalities which have occurred, probably depend on a commencing degeneration in the cells while waiting for fertilization. In very young sacs the synergid nuclei were placed in the upper part of the cells.

The antipodals among the *Meliaceae* are three; exceptionally I have seen them multiplied, as in *Chisocheton amboinensis*, fig. 25 I. Their position varies, sometimes they lie in a row, as in fig. 25 F of *Melia Azeradach*, sometimes two are at the bottom and one above (fig. 23 F). The customary position with one cell at the point of the sac and two abreast above it, I have observed in most of the species (see figs.). Generally the antipodals in this family do not persist for any length of time, but soon become absorbed. In somewhat older embryo sacs the antipodals have, as a rule, been lacking or degenerated. In *Melia*, some *Dysoxylum*, and *Chisocheton*, a. o., they have been more vital (see figures).

The polar nuclei were in excellent condition and observed in contact in a great number of species; see figs. As a rule they meet in the middle part of the sac. Their fusion product, the primary endosperm nucleus, has been observed in some species, e. g. *Chisocheton* (fig. 25 K), *Dysoxylum alliaceum* (fig. 25 H), *Aglaia eximia* (fig. 23 M), and *Sandoricum Koetjape* (fig. 25 G).

As is commonly the case, the nucellus gets absorbed round the E. S., during the development of the latter, especially in weak nucelli, as in *Aglaia* (fig. 25 A). In *Sandoricum* the nucellus round the E. S. consists of hypertrophied cells of plasma thinness (fig. 24 O, 25 G).

Fertilization. Endosperm. Embryo.

As to the pollination in *Meliaceae*, HARMS says (1896): »Genauere Angaben fehlen.« SCHNARF (1931) reports that *Carapa* has porogamy. I am now in a position to enlarge, to some extent, our knowledge of the fertilization in this family.

The *conducting tissue* begins on the papillous or pilose stigma. Often a whorl of long hair borders the rounded stigma, as shown by the figures of *Dysoxylum*, *Capara*, *Swietenia*, and others. At times, the whole stigma is pilose. (*Melia*, *Aglaia*, a. o.) A detail of the hair whorl is given in fig. 26 H. In the stylar canal the epidermis is more or less hairy or papillous, as the figures 26 E and I show. At the time of the pollination, the placenta is, in *Turraea*, covered with a pilosity, as shown in fig. 18 D, 26 G.

An obturator exists in *Chukrasia*, but also in some other genera the funicle gets more or less swollen, obturator-like (*Swietenia*).

Fertilization. In the above chapter I have mentioned a number of ready-built embryo sacs but in only a few of them were there signs of pollination or of fertilization. I cannot give any definite explanation why this is so. There may be various causes. In the material studied I have not found that the pollen was bad. The species have bisexual flowers. There are, however, tendencies to dioecism or polygamy. I have in several species seen that the pollen in the anthers de-

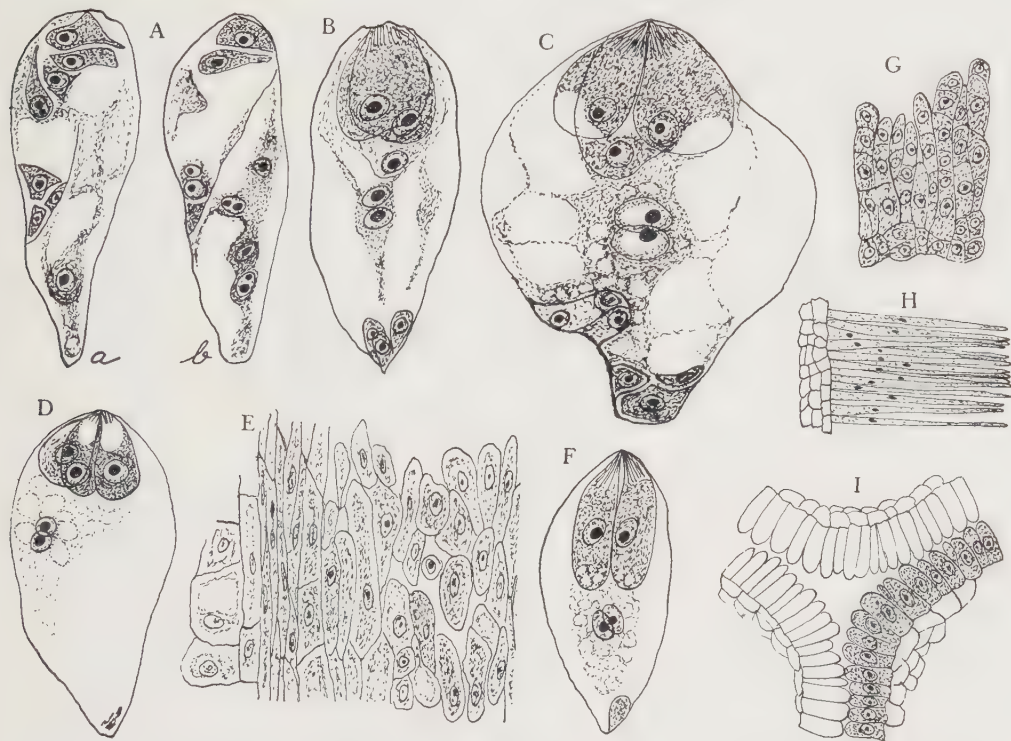


Fig. 26. *A a-b Aphanamixis grandifolia.* Two embryo sacs. Two consecutive sections. $\times 400$. *B Walsura pinnata.* E. S. $\times 485$. *C Aglaia Eusideroxylon.* E. S. Nucellus cells entering the sac. $\times 600$. *D Aglaia rufa.* E. S. $\times 485$. *E Dysoxylum Blumei.* Conducting tissue in the stylar canal. $\times 300$. *F Dys. urens.* E. S. $\times 485$. *G Turraea obtusifolia.* Hair on the placenta. $\times 300$. *H Dysoxylum macrothyrsus.* Hair on the stigma. $\times 300$. *I Dys. alliaceum.* Papillous epidermis on the placenta. $\times 300$.

generates, at least in certain flowers of *Dysoxylum alliaceum*, and still more in *Aphanamixis*. HARMS (1896, p. 264) says that this genus shows a marked dioecism. The flowers, in this family, occur in rich inflorescences and are built for insect pollination. Nectaries commonly occur, as is mentioned above. Very seldom, however, have I seen any pollen on the stigmata, even if these have been quite vital. The feeble pilosity on the stigmata, however, soon seems to dry up in the warm climate. At the time of the ripening of the E. S., this has in many flowers been resinous, and thus the stigma has been unfit for pollen germination.

In the following species I have found signs of fertilization, viz. in *Swietenia macrophylla*, *Turraea floribunda*, *Melia floribunda* and *Azedarach*, *Sandoricum borneense*.

Many fertilized ovules have been seen in *Swietenia macrophylla*. Almost every ovule in the multiovular ovaries was pollinated. The passage of the tube over



Fig. 27. A, D *Melia floribunda*. A Pollen tubes in style and ovary. $\times 25$. D Pollen tube. 2-celled embryo. 4-nuclear endosperm. $\times 350$. B *Walsura quadrilocularis*. Young seed with endosperm. No embryo. C *Swietenia macrophylla*. Fertilized egg cell. Endosperm 8-nuclear. $\times 250$. F *Melia Azedarach*. Embryo. Nuclear endosperm. $\times 250$. G-I *Turraea floribunda*. G Pollen tube. Egg cell fertilized. 64-nuclear endosperm. $\times 250$. H-I Transverse sections of E. S. with 64 endosperm nuclei. H through the egg apparatus, the egg cell fertilized. $\times 600$.

the hairy obturator and through the micropyle could easily be followed in many ovules (fig. 27 E). Here, too, porogamy prevails. In fig. 27 E a fertilized but still undivided egg cell is visible with two nucleoli in the nucleus. Endosperm of eight nuclei had already been formed, from which it is clear that the endosperm nucleus divides before the egg nucleus. Later stages were not at my disposal. No embryos were found. Almost all the embryo sacs in one and the same ovary

showed the same development stage as the fig. and contained eight endosperm nuclei. The antipodals were lacking.

As to the fertilization in *Carapa*, see above. Also *Turraea floribunda* has shown many fertilized ovules and good nuclear endosperm in several embryo sacs. Fig. 27 G shows a pollen tube in the micropyle and embryo sac. The egg nucleus was no doubt fertilized, because two clear nucleoli were visible. Sixty-four endosperm nuclei were found in the sac. This ovule was the upper one in the chamber. Otherwise the lower ones were, as a rule, fertilized and tended to further development, whereas the upper ones were smaller, unfertilized and tended to abortion. In other sacs in the same ovary, 16 endosperm nuclei were found. Thus we find that also in *Turraea* the division of the endosperm nucleus is previous to that of the egg nucleus. The figures 27 H-I are cross-sections through the upper and middle part of an embryo sac in the same species. In the former the disorganized synergids and the egg cell are visible. Here, too, the nucleus of the latter contained two nucleoli and was thus probably fertilized. This sac, too, contained 64 endosperm nuclei. Porogamy occurs in *Turraea* also.

Melia Azedarach and *floribunda* have also been fertilized. Fig. 27 A shows the abundance of pollen tubes and their passage in the style, on the placenta and in the micropyle. Also in these species the lower ovules get fertilized and further developed. The upper ones are smaller and do not seem to get any pollen tubes, although they contained fully developed embryo sacs. The pollen tubes grow ectotropously on the papillous conductive tissue in the style and on the placenta and go straight to the micropyle. Sometimes, however, they seem to go endotropously in the placenta tissue, before they reach the micropyle. Porogamy prevails here too. Fig. 27 D shows a massive tube entering the micropyle and the nucellus which latter gets disorganized, so that black bodies remain.

In *Melia* the egg and endosperm nuclei divide almost simultaneously as is seen in fig. 27 D, where a 2-celled embryo and four endosperm nuclei occurred. The antipodals persist a longer time in this genus, as the figure shows.

No doubt double fertilization takes place in this family.

Also in *Melia Azedarach* I have noted that the course of the pollen tubes is quite the same as in *floribunda*.

The *Melia* species have often failed to produce any embryos, although fertilized. Of the egg apparatus only the almost empty cellulose walls then remained, and the endosperm nucleus had not divided. In many ovules, however, the latter divides and gives rise to a nuclear endosperm. Such ovules I have often seen in these *Melia*. They grow out unfertilized, or else fertilized but lacking embryos. In some of them a quite normal embryo arises, as in fig. 27 F, but this seems later on to abort, at least in certain cases. Fig. 28 H is a young embryo from a developed seed. The embryo lay quite free in the upper part of an embryo sac which, otherwise, contained only a very thin plasma veil along the wall with but a few scattered endosperm nuclei. No nutrition existed, either in the embryo sac or in the nucellus. Such an embryo is no doubt destined to abort. I have seen

many seeds of that type, with a small exhausted embryo of a few cells and a thin nuclear endosperm. The E. S. in these seeds extends into the chalaza.

Also *M. Candollei* has a nuclear endosperm and is in other respects, as well, similar to the rest of the genus. No embryo has been observed.

Thus, in these *Melia* species partial parthenocarpy, at least, seems to exist.

The upper ovule in the ovary chamber in *Melia* does not grow out. After the embryo sac is built, they abort. The embryo sac hypertrophies and the nucellus protrudes through the micropyle. Fertilization or embryo formation does not take place, but an ephemerical nuclear endosperm of a few nuclei may be found. I saw in such an abortive ovule six endosperm nuclei.

Also in *Sandoricum borneense* signs of fertilization have been observed, in an embryo sac with a disorganised synergid, fig. 28 A. The polar nuclei had not fused, the antipodals were in absorption.

The endosperm has previously been touched upon. Double fertilization no doubt exists in *Meliaceae*, although I have not seen the nucleus fusion. The division of the primary endosperm nucleus is evidently independent of fertilization or division of the egg cell. In many embryo sacs without any trace of fertilization I have seen endosperm. The earliest stage observed was a 2-nuclear endosperm in *Swietenia macrophylla*, seen in several cases (fig. 28 B). Even the next stage, 4-nuclear endosperm, has been noted in this species as well as in *Melia floribunda* (fig. 27 D). I have observed 8-nuclear endosperm in many embryo sacs of *Swietenia macrophylla*, and several sacs with 16- and 64-nuclear endosperm in *Turraea* (fig. 27 G-I). Nuclear endosperm also exists in *Dysoxylum*, *Aglaia*, and *Walsura* (fig. 27 B). Embryos have been found in the two first-mentioned genera.

Fig. 28 E *a-b* represent the upper and lower part of an E. S. in *Dysoxylum alliaceum*. A young embryo lies embedded in endosperm which has begun to get organized. This process, mentioned also by other authors, consists in the endosperm becoming cellular in only one stratum, the so-called »endosperm cap» (GIBBS 1907, p. 34). GIBBS has noted this in *Alsinoideae*, and ROCEN (1927, p. 89), in *Heliosperma* of the same family as well as in the family *Nyctaginaceae* (l. c., p. 35). In *Dysoxylum* the cell wall still seemed to be lacking towards the sac. In the lower part of this the endosperm was still nuclear (fig. *b*). Fig. 28 F is an example of mitotic division in the endosperm in the same species.

Fig. 28 C, G are sections of embryos in *Aglaia eximia*. The cotyledons are large and wing-like. The endosperm seems to become cellular very slowly, if at all, as in later stages there was still found a thin layer of wall plasma with indistinct walls between the endosperm nuclei (fig. 28 C).

In a young seed of *Walsura quadrilocularis* a nuclear endosperm has been noted, but no embryo (fig. 27 B). Also *Carapa* has an endosperm of the same type (SCHNARF 1931).

The embryo formation has been mentioned above. The egg cell divides later than the primary endosperm nucleus. The first division of the former is a transverse one, as is shown in fig. 27 D. I have not observed the next stages. The

dermatogen is already formed in the figures 27 F, 28 E, H. Parthenocarpic development has been established in *Melia*, *Swietenia*, *Walsura*, and others. About the embryo development in *Carapa moluccensis* KARSTEN (1891, p. 22) writes as follows: »Der Embryo liegt, den Nucellus bereits hinter sich lassend, unmittelbar an der mikropyle und streckt die wurzelende aus derselben hervor. Der Stammvegetationspunkt sendet eine, durch die nur schwach angedeutete Grenzlinie, als

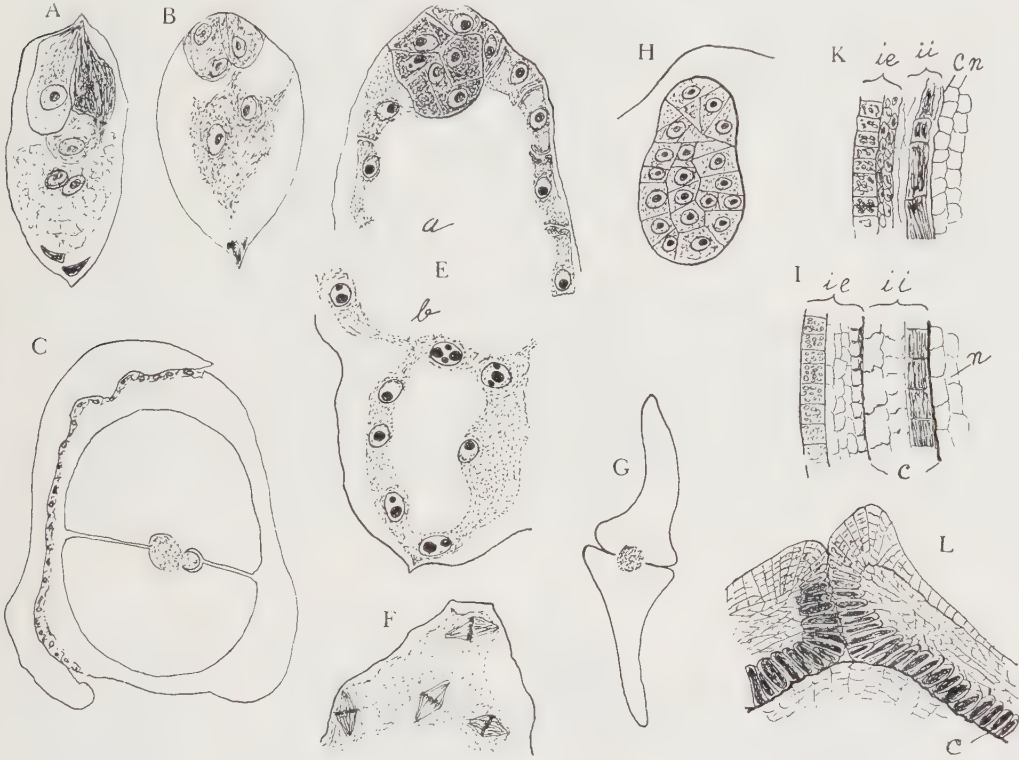


Fig. 28. *A* *Sandoricum borneense*. Fertilized E. S. $\times 485$. *B* *Swietenia macrophylla*. 2-nuclear endosperm. $\times 400$. *E-F* *Dysoxylum alliaceum*. *E* *a* Embryo. Endosperm cap. *b* the lower part of the same sac with nuclear endosperm. $\times 300$. *F* Mitotic division in the endosperm. $\times 300$. *C, G* *Aglaia eximia*. Longitudinal and transverse sections of embryo. $\times 30$. *H-L* *Melia Azedarach*. *I* Seed testa. *K* The same, later. *ie* outer, *ii* inner integument, *c* cuticle, *n* nucellus. $\times 70$. *L* Inner epidermis of the inner integument gets a peculiar structure; *c* cuticle. $\times 100$. *H* Embryo. $\times 250$.

aus zwei Anlagen verwachsen kennliche Cotyledoner-Masse als Saugorgan in den Embryosack hinein. Endosperm wird mit Ausnahme einiger in den Ecken unmittelbar am Embryo ansetzender Zellen nicht gebildet ... Der Nucellus selbst wird gänzlich verdrängt und die gesamte Höhlung des Embryosackes von der Cotyledoner-Masse eingenommen.» He then describes the further growth of the embryo in this viviparous plant up to the moment when it gets loose and falls to the ground.

As to embryo and seed in this family, see further KING (1895) and HARMS (1896).

The seed testa.

»Entwicklung der Samenschale fast unbekannt», says NETOLITZKY (1926, p. 181) of the family *Meliaceae*. He then describes the seed testa in a number of species. About its development I can report some observations made on *Melia*.

A somewhat earlier stage is visible in fig. 28 I. The outer integument consists of three layers, viz: The outer epidermis of cubic cells, with resin grains; further several small-celled strata, varying somewhat in number, round the seed; finally a weak, small-celled epidermis. A weak cuticle separates the inner from the outer integument. The inner integument has some wide-celled, plasma-thin outer strata, varying somewhat in number round the seed, and an inner epidermis of cubic cells, which already in earlier stages become strongly green-coloured. About its chemical condition I can say nothing. It has evidently some protective task. Fig. 28 L shows, in a later stage, the appearance of this epidermis in the vicinity of the micropyle. The cells are here palisade-like, oblong, but round the nucellus lengthened in a periclinal direction (fig. 28 K). The nucellus is covered with a thicker cuticle. A later stage of the testa is shown in fig. 28 K. Of the inner integument there remains only the green layer mentioned above, whereas the outer strata are pressed together. The outer integument is resinous. Thus the mature seed testa in *Melia* consists of the outer integument plus the inner epidermis of the inner integument.

The pollen development.

Carapa guianensis forms, according to KRETZKY-DERSCH (SCHNARF 1931), only one row of the pollen mother cells in each pollen sac; the pollen division is simultaneous, and the tapetum is of the customary type. Of *Carapa* I have not had at my disposal any earlier stage than 1-nucleate pollen. When mature, they are 2-nucleate and filled with albumen. The statement about the tapetum is verified by my investigations. I can add that at the time of the pollen maturity there is a well developed fibrous stratum in the anther wall, as is the case in all the species of this family whose pollen development I have studied. Also the tapetum is in all of the species a secretive one with one- or several-nucleate cells. During pollen formation the tapetum gets absorbed.

In several species, I have seen the pollen mother cells in only one row, e. g. in *Turraea obtusifolia* (fig. 29 A). In *Chisocheton* the pollen sac is divided into small partitions, with a few pollen mother cells in each (fig. 29 B). Comp. HARMS (l. c.).

The nucleus of the pollen mother cell passes through the heterotypic division without any wall formation. I have seen this simultaneous pollen formation in the following species: Fig. 29 C is a heterotypic metaphase and fig. 29 D dyad nuclei in *Melia Azedarach*. Asynchronous division has been seen in the pollen sacs.

In fig. 29 K of *Dysoxylum alliaceum* four tetrad nuclei have just arisen through homotypic division, and the same stage is shown in fig. 29 I of *D. nutans*.

Pollen tetrads have been observed, besides, in *Dys. ramiflorum* (fig. 29 H) and *Blumei*, *Cedrela Glaziovii*, *Walsura pinnata*, and others. Of the last-mentioned species all stages of pollen development have been found in the ma-

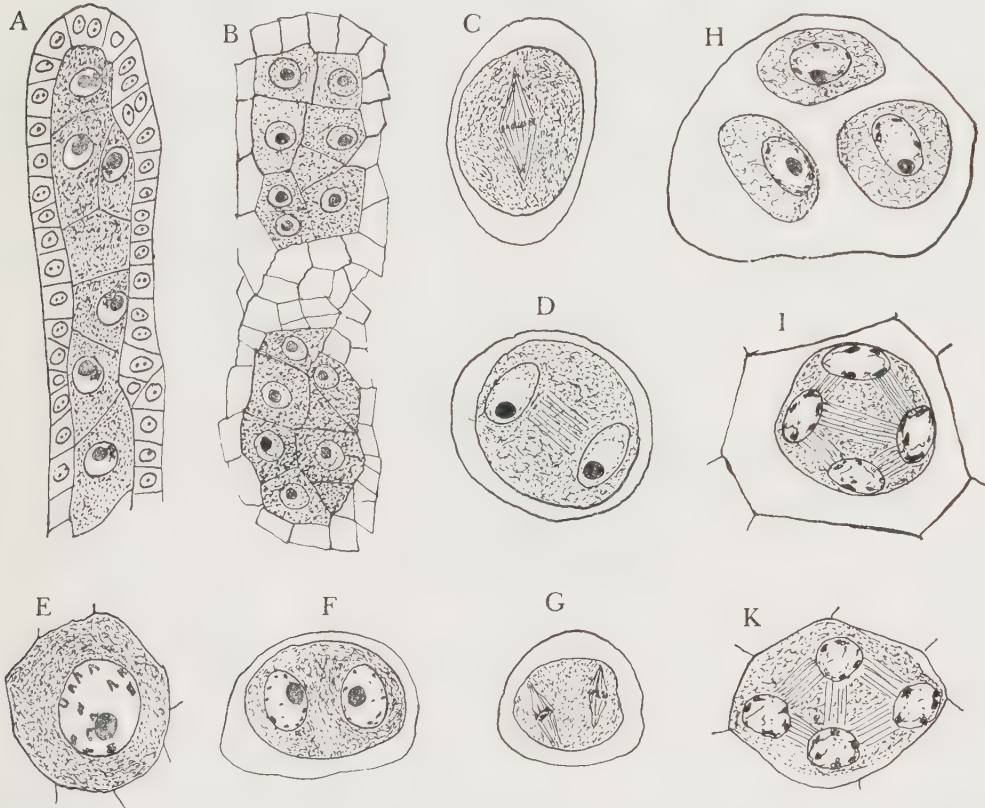


Fig. 29. *A Turraea obtusifolia*. Transverse section of pollen sac with the pollen mother cells in a row. $\times 300$. *B Chisocheton divergens*. The pollen sacs are divided into small rooms with a few pollen mother cells each. $\times 485$. *C-D Melia Azedarach*. *C* Heterotypic spindle. *D* Dyad nuclei. *E-G Walsura pinnata*. *E* Pollen mother cell in diakinesis, about 13 gemini. *F* Dyad nuclei. *G* Homotypic division. *H Dysoxylum ramiflorum*. Pollen tetrad. *I Dys. nutans*. Homotypic telophase. *K Dys. alliaceum*. Ditto. *C-K* $\times 900$.

terial. This species has indeed, as is often the case in *Meliaceae*, ten stamens in the flower; in one and the same flower, however, there were found: pollen mother cells, heterotypic division in all phases, dyad nuclei, homotypic division figures from different stages, and finally tetrads and pollen formation. Fig. 29 E shows a pollen mother cell in diakinesis, with 13 or 14 gemini. In fig. 29 F dyad nuclei in interkinesis are visible, and in fig. 29 G the homotypic metaphase of the same species.

The wall formation takes place, so far as I could gather, quite regularly according to the cell plate type (YAMAHA 1926). By degrees the pollen cells become free. 1-nucleate pollen has been seen in a great number of species. It has then no reserve food. The nucleus lies embedded in plasma, but otherwise the grain is empty (fig. 30 C). The nucleus then divides, and as long as the anthers are unburst, the pollen in *Meliaceae* continues to be 2-nuclear. The grains are now stuffed with reserve nutrition (fig. 30 B), but in spite of that the nuclei are distinctly prominent in the shape of two black bodies, so that I have been able to count them. Because of the systematical value this detail possesses, according to several authors, I spent some time counting the nuclei in a great many species, selecting as mature pollen as possible.

Fig. 30 B shows a pollen grain in *Melia Candollei*. The large vegetative nucleus with its nucleolus is visible, and also, as is generally the case, the spindle-shaped

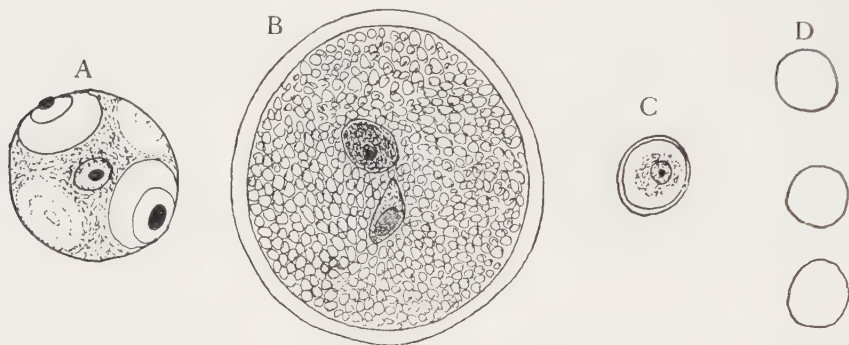


Fig. 30. A *Carapa guianensis*. Pollen grain. B *Melia Candollei*. Pollen grain, 2-nuclear. C *Aglaia argentea*. 1-nuclear pollen. D *Aglaia Ganggo*. Three pollen grains. All figs. $\times 900$.

generative cell with its nucleus undivided. Here, just as in several other species, the green-coloured cellulose membrane round the generative cell served excellently to decide whether 2-nucleate pollen has still been present. The green membrane has clearly appeared in the yellow-coloured nutrition mass. SCHÜRHOFF (1924, p. 735), too, mentions the trouble that the reserve nutriment in the pollen gives when the object is to count the nuclei, and emphasizes the fact that the generative nucleus divides only a short time before the opening of the anthers. I have, however, in several cases seen only 2-nucleate pollen in pollen sacs whose fibrous stratum was fully developed, and accordingly the sac was at the stage immediately prior to opening. It is not to be assumed that this pollen would be 3-nuclear before spreading.

The author cited above gives an account of the pollen in the order of *Geraniales* and has found it to be 3-nuclear, except in *Tropaeolaceae* and *Simarubaceae* which have 2-nuclear pollen. He considers that this indicates the uniformity of that order. The *Meliaceae* is also referred to the same order but this family has hitherto been without reports as to the number of the nuclei in the pollen. It

appears from the above that in this respect, too, the family agrees with *Simarubaceae*, and also with the family *Burseraceae* whose pollen has not hitherto been investigated (see below).

The size of the pollen grains varies considerably in *Meliaceae*. Most of the genera have rather large grains of the same appearance as in *Melia*, fig. 30 B. *Turreae obtusifolia* has even somewhat larger ones. The grains in e. g. *Carapa* (fig. 30 A) and *Sandoricum* are medium-sized, very small in *Aglaia*. The three grains in fig. 30 D represent *A. Ganggo*, and I have seen that *A. odoratissima* has similar ones. *A. argentea* has slightly larger grains (fig. 30 C). There is, indeed, a remarkable difference between the figures 30 B and C-D, designed on the same scale. The whole of the grain in *Aglaia* is not much larger than the nucleus in the *Melia* grain!

The pollen in *Carapa* has four rounded plates surmounted by a little round wart (fig. 30 A).

EICHLER (II, 1878, p. 328) says he is not confident which circle the five stamens in *Aglaia* belong to. I have established that they belong to the outer circle, whereas the inner one is lacking.

Simarubaceae.

This family is one of the smaller ones in the order of *Terebinthales*. It comprises 32 genera with about 200 species, according to HARMS (ENGLER and PRANTL 1931). The family is on the whole a tropical one, widely spread in all continents but with its centre in tropical America. »Im allgemeinen sprechen diese Verbreitungsverhältnisse dafür, dass die *S.* eine sehr alte tropische Pflanzenfamilie sind, deren jetzt lebende Gruppen Reste von ehemals reicher entwickelten Typen sind» (ENGLER 1896, 1931). *Suriana maritima* is a shore plant in all tropical lands from Florida and the West Indies eastwards to the Marshall Islands. Only a few species are spread outside the Tropics, e. g. *Holacantha Emoryi* in sub-tropical North-America, or *Ailanthus glandulosa* which is hardy as a park-tree so far from the Tropics as in our own regions.

I had at my disposal more or less material of 15 species out of 11 genera. Two of these were of male character with rudimentary gynaecia. The material includes also the systematically still doubtful *Picrodendron baccatum* (see below).

The species investigated are the following, according to ENGLER (1931):

I. Surianoideae.	<i>Brucea amarissima</i> (LOUR.) MERR.
<i>Suriana maritima</i> L.	<i>Picrasma javanica</i> BL. (♂).
	<i>Ailanthus altissima</i> SWINGLE.
	» <i>glandulosa</i> DESF.
II. Simaruboideae.	» <i>malabarica</i> DC.
<i>Samadera indica</i> GÄRTN.	» <i>moluccana</i> DC. (♂).
» <i>mekongensis</i> ENGL.	IV. Irvingioideae.
<i>Quassia amara</i> L.	<i>Irvingia malayana</i> OLIV.
<i>Harrisonia Brownii</i> JESS.	VI. Alvaradoideae.
<i>Holacantha Emoryi</i> A. GRAY.	<i>Alvaradoa amorphoides</i> LIEBM.

Picrodendron baccatum (L.) KRUG ET URB.

Of *Holacantha* and *Alvaradoa* there were only embryo stages in the material. The material originates from the following localities. From the Botanic Gardens at Buitenzorg: the *Samadera* species, *Harrisonia Brownii*, *Brucea amarissima*, *Picrasma javanica*, *Ailanthus malabarica* and *moluccana*, *Irvingia malayana*, and

Picrodendron baccatum. *Suriana maritima* was collected in Madagascar, *Quassia amara* in Georgetown, Brit. Guiana, *Holocantha Emoryi* in Arizona, *Ailanthus glandulosa* ♀ in the Botanic Garden, Copenhagen, ditto ♂ and *A. altissima* in the Botanic Gardens of Palermo and Vienna. *Alvaradoa amorphoides* is from Mexico.

Simarubaceae, like *Burseraceae*, is nearly related to the *Rutaceae*. *Simarubaceae* has, however, as ENGLER (l. c.) states, no such characteristic anatomical criterion as those two families, viz. the *Burseraceae* balsam and resin, the *Rutaceae* ethereal oil. BOAS (1913, p. 303) has also pointed out the same lack of characters throughout this family. The most characteristic traits in *Simarubaceae*, although they do not exist in all the genera, are: intrastaminal disk, at times gynophor-like, ligula at the base of the filaments (see figs. in ENGLER and PRANTL), epitropous ovules, and bitter, extractive substances in the wood (e. g. *Quassia amara*).

In the present investigation I have also included *Picrodendron baccatum*, the placing of which has hitherto been uncertain. ENGLER (1896) calls this genus a »zweifelhafte Gattung der *Simarubaceae*, deren systematische Stellung noch nicht genau festgestellt werden kann». In the last edition of »Die natürlichen Pflanzenfamilien» (1931) *Picrodendron* is still associated with this family but as an »auszuschliessende Gattung». The first description of this plant was given by LINNAEUS, as *Juglans baccata* (FAWCETT and RENDLE 1917, p. 268). PLANCHON (1846, p. 579) founded the genus *Picrodendron*. He knew no flowers, but on account of fruit and vegetative characters he allied the plant to the family *Simarubaceae*. Several authors have, later on, written on this somewhat doubtful genus (see ENGLER, l. c.). BOAS, for instance (l. c., p. 308 and 314), points out the similarity to *Irvingia* in the structure of the leaf stomata and in the occurrence of mucous vesicles in the tissues. Numerous vesicles occur in *Picrodendron* also in the gynaecium (fig. 32 B, E), but not in *Irvingia* (fig. 31 F-G). I have, however, seen smaller ones also in the ovary of the latter, in later stages. Only the group *Irvingioideae* in the family has mucous glands, whereas this group, as well as *Picrodendron*, lacks such secretion vesicles (resin, oil) which occur in other genera. Also in the number of the carpels (2) *Picrodendron* agrees with *Irvingia*, whereas the former has biovular, the latter uniovular chambers in the ovary. A more detailed diagnosis of the genus *Picrodendron* which occurs also in the last edition of the »Pflanzenfamilien», is given by FAWCETT and RENDLE (1917, p. 268). One, rather important systematic detail, seems, however, to have been erroneously described by them, viz. the position of the ovary in relation to the sepals. The authors note »ovary inferior», and in the consequence of this ENGLER has »Ovar unterständig», but from my figures 32 A-B it is evident that the ovary is above the sepals. The minute glands at the base of the sepals mentioned by FAWCETT and RENDLE are also to be seen in my figure 32 B. The sepals grow up close to the ovary (fig. 32 A) but this is quite free. FAWCETT and RENDLE mentioned also that *Picrodendron* has an obturator (about this more below) and state that the genus, on account of this and other characters, shows affinity to *Euphorbiaceae*. PAX and HOFFMANN (ENGLER and PRANTL, 2nd edition) do not agree with the former

two authors in this respect, referring among other things to the »unverständigen» ovary. As this character thus falls off, and *Picrodendron*, as well as *Euphorbiaceae*, has an obturator and the same epitropous placentation, a junction with the latter family may be possible. As is shown below, *Picrodendron* does not

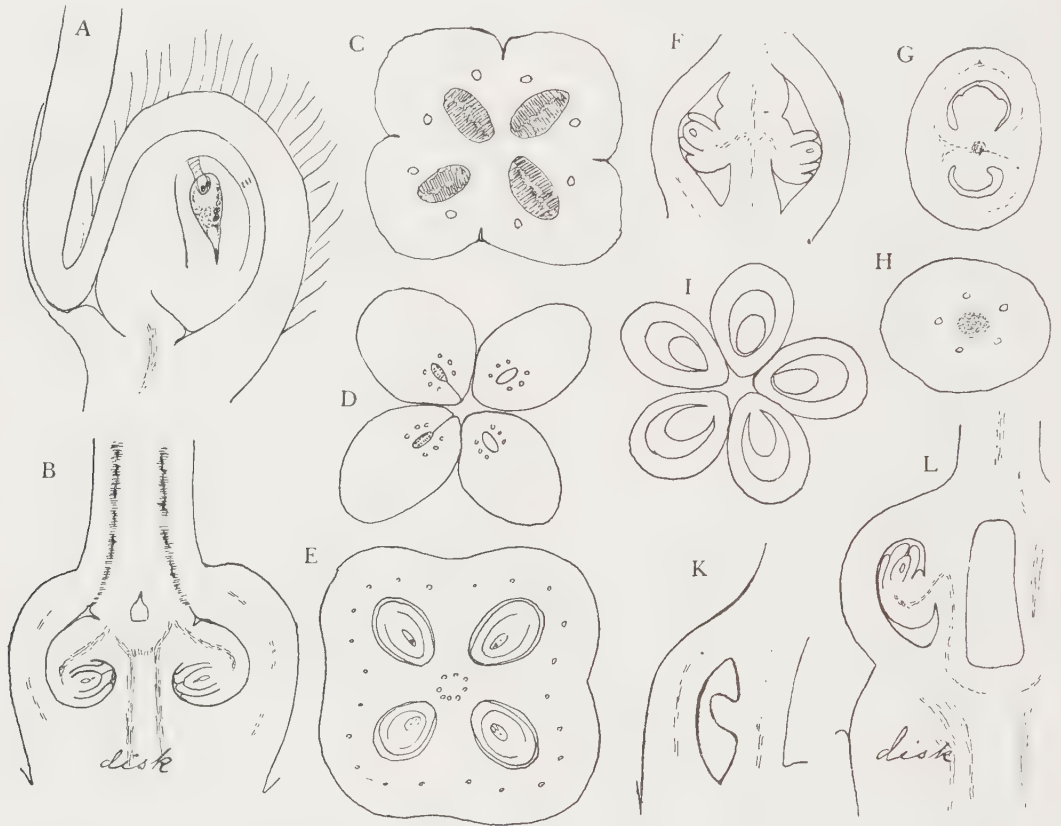


Fig. 31. *A* *Suriana maritima*. Longitudinal section through one of the ovaries. Unitegmic. The micropyle not hit by the knife. $\times 70$. *B-E* *Harrisonia Brownii*. *B* Longitudinal section through disk, ovary and lower part of the style showing the apotropous ovules, the styler canals, and vascular strands. $\times 40$. *C* Transverse section of the style showing the styler canals with palisade epidermis (see fig. 39 *B*). $\times 100$. *D* Transverse section through the basal part of the style with free carpels. $\times 35$. *E* Transverse section of ovary. $\times 35$. *F-G* *Irvingia malayana*. *F* Longitudinal, *G* Transverse section through the ovary. $\times 70$. *H-L* *Quassia amara*. *H-I* Transverse sections through style and ovary; in the latter the carpels free. Conducting tissue in the centre of the style. $\times 70$. *K* Longitudinal section of young ovary chamber showing the ovular papilla. $\times 70$. *L* Later stage. $\times 35$. Vascular strands designed.

deviate, however, in embryological respects, from other *Simarubaceae*, wherefore this genus can also be placed in the vicinity of *Irvingia*, as is said above.

Little is said in the embryological literature about the development of the *Simarubaceae*. Thus SCHÜRHOFF (1924, p. 732) reports as to *Ailanthus glandulosa* that this species »ist diözisch. Die reifen Pollenkörner der männlichen Exemplare

zeigen nur zwei Kerne, die generativen Zelle ist deutlich erhalten. Die sogenannten »zwittrigen Exemplare« zeigten in den Antheren keine Archesporentwicklung, sondern die Antheren bestanden ausschliesslich aus vegetativen Zellen; es handelte sich also hier um Staminodien. Die weibliche Haploidgeneration ist völlig normal, das Archespor ist einzellig, der Embryosack achtkernig.» The same author reports, later on (1926, p. 587), that the endosperm in this species is nuclear.

Gynaeceum. Genesis, number and orientation of the ovules.

ENGLER (1931) describes the flower and gynaeceum in the family. The flowers have often only the one sexual organ fully developed and fertile, whereas the other is rudimentary or quite lacking. As is mentioned above, the *Simarubaceae* have a disk which is annular, cup- or gynophor-like (fig. 31 B, L); see further figs. in ENGLER.

The gynaeceum in *Simarubaceae* is rather varying in structure. As to the number of the carpels they are 1—5, seldom more. In the genera here concerned the number is: in *Suriana* 5, *Samadera* 3—5, *Quassia* 5 (fig. 31 I), *Harrisonia* 4—5 (fig. 31 C-E), *Ailanthus* 5—6 (fig. 32 H), at times fewer (*malabarica* 3). *Irvingia* (fig. 31 G) and *Picrodendron* (fig. 32 E) have two carpels. *Brucea* has 4, *Alvaradoa* 2—3, *Holacantha* about 6, a. s. f.

Also as regards the relation of the carpels to each other there is a good deal of variation. Only *Suriana* is quite apocarpous (fig. 31 A). *Irvingia* and *Picrodendron* have wholly syncarpous ovaries, as the longitudinal and transverse sections, figs. 31 F-G, 32 B, E, show. Also the styles in these genera are quite united. *Harrisonia* has not the carpels entirely united. In one zone at the base of the styles the carpels are free, as fig. 31 D shows. The free zone is in the longitudinal sections, figs. 31 B, 34 A, marked by a little space. *Samadera* and *Quassia* have the carpels in the ovary free but the styles are grown together (fig. 31 I-H). In *Holacantha* the carpels are united at the base and in the style. *Brucea* has at times quite apocarpous gynaeceum (fig. 34 F), at times, as in *Holacantha*, the carpels united at the base. No styles exist in *Brucea*, but the rather long and thick stigmata are placed directly on the ovary and are strongly bent back, as fig. 34 F shows. Fig. 32 G-L show longitudinal and transverse sections of the gynaeceum in *Ailanthus*. The carpels in the ovary are free, as is seen in fig. 32 I-K. The ovaries are flattened, with the outer and upper border, in later stages, more or less wing-like (fig. 32 I), and at the base surrounded by the 10-lobate disk (fig. 32 L). The carpels in *glandulosa* are grown together into one style but this is furrowed on the outside (fig. 32 H), the stigmata are rather large, bent outwards and more or less divided into smaller, irregular lobes (fig. 32 G). The gynaeceum in *malabarica* is similar to that of *glandulosa* with the exception that the styles are free and the carpels 3 in number. The style in *Suriana* is basally fixed (fig. 31 A), this being caused by a strong, one-sided, dorsal growth of the carpel.

The vascular system in the gynaecium is drawn in several figures (31, 32). A strong vascular strand goes through the placenta and further into the ovules (e. g., fig. 32 F).

PAYER (1857, p. 109) describes in detail the origin and the development of the gynaecium in *Ailanthus glandulosa*, with detailed figures: »Lorsque toutes



Fig. 32. A-E *Picrodendron baccatum*. A The entire gynaecium and the sepals. $\times 4$. B Longitudinal section through the ovary showing the epitropous ovules, obturator, and hair cushions on the placenta, the mucous vesicles in the ovary wall and the minute glands at the base of the sepals. $\times 35$. C-E Transverse sections: C through one of the stigmata with two mucous vesicles, D through the style, showing the conducting strand in the centre, E through the ovary, showing biovular rooms, the placenta hairs and the mucous vesicles. $\times 35$. F *Samadera indica*. Longitudinal section through ovary with conducting tissue and vascular strands. $\times 40$. G-L *Ailanthus glandulosa*. G-I, L Transverse sections through: G the lobate stigma, H style showing conducting strands in the centre, I free carpels in the ovary, L the basal part of the ovary showing the flattened carpel (c) and the lobate disk (d). K Longitudinal section through gynaecium, showing the course of the pollen tube. G-L $\times 35$.

les étamines sont nées, on voit poindre, dans l'*Ailanthus glandulosa*, sur le sommet du réceptacle, qui ressemble alors à une terrasse pentagonale élevée au centre de la fleur, cinq mamelons superposés aux pétales. Ces cinq mamelons sont les rudiments du pistil. Ils sont complètement libres les uns des autres, et le seront toujours. D'abord hémisphériques, ils prennent bientôt chacun la forme d'un fer

à cheval dont la courbure est la partie la plus élevée, et dont les branches, au lieu de rester parallèles, convergent l'une vers l'autre et tendent à se réunir. Cette réunion s'effectue en effet plus tard, et chacun des mamelons primitifs, qui est devenu un carpelle, présente sur sa face ventrale une large ouverture, qui est bornée à la partie inférieure par une sorte de parapet, et à sa partie supérieure par un tubercule, rudiment du style. Cette ouverture se rétrécit peu à peu par suite du rapprochement de ces deux bords latéraux, et finit par ne plus former qu'une fente très étroite. C'est à la base de cette fente, sur la paroi interne de cette sorte de parapet qui la limite à la partie inférieure, que naît un ovule anatrope.»

As regards the number of the ovules, their placentation, orientation and shape the following may be noticed.

More than two ovules in each cell do not exist in this family. Of the genera studied *Suriana*, *Alvaradoa* and *Picrodendron* have two ovules, all others only one in each cell. Their orientation is stated in the systematical manuals to be an epitropous one all over. I have, however, found some deviations in this respect.

The apocarpous *Suriana maritima* has in each of the five free ovary chambers two collateral ovules with basal placentation, as fig. 31 A shows. This is, however, only apparent. The ovary grows even in early stages one-sidedly in such a manner that it becomes quite unsymmetrical, and then the dorsal side grows stronger, so that the fixed points of the style and ovule are removed down to the ventral side of the carpel, as fig. 31 A shows. The fixed point of the style really represents the top of the ovary which is thus turned half round, so that the micropyle is directed upwards instead of downwards as in earlier stages. The further development of nucellus and ovule in *Suriana* is rather interesting. At the time shown in fig. 31 A a vivid cell division takes place in funicle and raphe so that they become strongly swollen, as is shown in fig. 41 A. Because of this development the nucellus gets right angles to the funicle. The former now shows a commencing curvature, too. The ovule is now hemitropous. The concave side becomes more and more filled with tissue and the nucellus gets more and more curved, so that, at the time of the development of the embryo, the nucellus has the shape shown in fig. 41 D. The ovule is now amphitropous (GOEBEL 1923, p. 1724). The embryo sac and embryo also get the same appearance (fig. 41 E). A rather thick strand of conducting tissue consisting of long, narrow cells leads into the concave side of the ovule (fig. 41 A, D). Thus we have seen that the orientation and the shape of the ovule in *Suriana* are considerably changed during development. *Suriana* much resembles other plants with curved embryo in that a special filling tissue is developed on the concave side. This tissue can, as GOEBEL points out, arise from the funicle, raphe, integument or nucellus, and also, as in *Centrospermae*, be filled with reserve nutriment (perisperm). No such occurs in *Suriana*. GIBBS (1907, p. 36 a. f.) describes the curved nucellus and embryo in *Alsinoideae*, and also the filling tissue on the concave side, similar to that of *Suriana*. COHN (1913, p. 71 a. f.) describes the same matter in the amphitropous ovule of *Atriplex hortensis*. The funicle is also here fixed at the concave side of the ovule. At the time of the

development of embryo and endosperm a special cell tissue, here arisen in the nucellus, radiates from the funicle (see his fig. 18 and 19). The embryo sac is also in *Atriplex* straight at first, but growing further down into chalaza it assumes the same amphitropous shape as the nucellus.

Inside the epidermis the ovary wall has, in *Suriana*, at the time shown in fig. 41 D, a special tissue consisting of empty cells in several strata with thick cuticle-like walls. The ovary in this species is hairy (fig 31 A).

Alvaradoa has, according to ENGLER, two basal ovules turned upwards, but with the micropyle directed downwards, and the raphe-sides facing each other. I had no early stages of this species.

In all other species investigated the ovules are fastened higher up in the chambers, and at least in later stages pendent. In *Samadera* a rather thick ovular papilla arises in the way shown in fig. 33 A. In that early stage it is turned upwards, later on it sinks to a pendulous position, the top, however, still bent upwards, as fig. 33 D shows. It has thus an epitropous situation. In *Quassia* a rather small papilla arises at the middle part of the placenta (fig. 31 K). Its orientation changes during development in the same manner as in *Samadera*. Thus the ovule is later on epitropous (fig. 31 L). *Harrisonia* has, in conformity with the former genera, uniovular chambers in, as is noted above, syncarpous ovaries (fig. 31 E). Fig. 34 A shows the apical, pendulous ovular papilla. Concerning the orientation of the ovule in this genus there occurs in the literature an error which I have here an opportunity to rectify. JADIN (1901, p. 258) reports: »Les carpelles sont unis, opposés aux pétales contenant chacun un ovule suspendu épitrope.» ENGLER (l. c.) says nothing about the orientation of the ovule, only that the ovary is »4—5 fächerig, mit je 1 vom Scheitel des Faches herabhängenden Samenanlage.» Nor does his figure of a longitudinal section through the gynaecium say anything about the matter, as no ovules are drawn there. PLANCHON (1846, p. 569) notes correctly that the seed is »ex apice loculi suspensum, campulitropum», but says nothing about the location of the micropyle. As is seen in my figs. 31 B and 34 B the ovules in *Harrisonia* are typically apotropous. The micropyle is placed inside and under the funicle. During the further growth of the ovule there is little space so that the top pushes against the placenta, wherefore the chalazal end is moved up to the upper part of the chamber. At the same time the ovule becomes campylotropous. Fig. 40 B is a section through a young fruit at the time of the embryo and endosperm formation. The ovule has now a rather peculiar position with the chalaza upwards. One could say that it is »upside down». The supposition may be expressed that JADIN had confused the chalazal end of the ovule with the micropylar one. Later the nucellus becomes still more curved so that the embryo becomes horseshoe-shaped (fig. 42 F).

I have not studied *Holacantha* in early stages. ENGLER states about this: »Samenanlage in jedem Ovarium an der Mitte der Bauchnaht hängend». Fig. 34 C shows the young, egg-formed, rather massive ovular papilla in *Brucea amarissima*. The ovule is epitropous and fills up the whole chamber (fig. 34 D, F). In the

flattened ovary of *Ailanthus glandulosa* there is a pendulous, epitropous ovule (fig. 36 A), filling up the whole cell. The syncarpous, rather small, 2-celled ovary of *Irvingia malayana* contains in each cell an also here epitropous, pendent ovule, fixed in the middle or lower part of the chamber (fig. 31 F, 39 E), not »oberhalb der Mitte des Faches«, as ENGLER has it (l. c.). The chambers are here rather spacious (fig. 31 F). Later on the ovules are lengthened and fill up the chambers (fig. 39 E). The funicle is then rather long and thin.

Picrodendron has, as is noticed above, 2 ovules in each partition (fig. 32 E), pendent from the middle part of the placenta (fig. 32 B). They are epitropous. A well developed obturator exists, and an abundant pilosity above the ovules is seen in the figure (see further below under the conducting tissue). *Picrodendron* has numerous mucus vesicles in the ovary wall (see figs.). A later stage of the ovary is shown in fig. 35 C. The chambers are voluminous, the ovules occur high up in the upper part and seem rather small in the wide room. They were unfertilized.

Nucellus. Archesporium. Integument.

The development of the young ovular papilla takes place in the following manner in the different genera.

Suriana maritima. Of this species I had no earlier stages than mature embryo sacs. The ovary and ovule have then the appearance shown in fig. 31 A. Above I have described the changing of the shape and position of the ovule during development in this species. The nucellus is seen in fig. 40 C. It consists of about five cell-layers round the embryo sac. This genus is unitegmic. The integument is about four layers thick, somewhat swollen at the point.

Samadera. Already in the young ovular papilla in fig. 33 A the archesporium is to be seen. Fig. 33 B is drawn from such a papilla. A subepidermal cell seems a little more advanced than others, but neither in this nor in other species of this family can one speak of a marked subepidermal archesporial cell. A somewhat later stage is drawn in fig. 33 C. The interior of the nucellus is occupied by a number of large vacuolized cells which have evidently been in growth. I counted in this ovule about 20 such cells. The inner integument was growing up round the nucellus. *Samadera* has thus a »many-celled archesporium«. Whether all these cells had an archesporial appearance even when hypodermal is a question that may remain open for discussion.

A similar structure is also seen in the young ovular papilla in *Turraea*, *Melia*, *Dysoxylum*, and others of *Meliaceae* (fig. 20, 21). Compare what is said about this matter above, page 48, as to *Turraea*. In fig. 33 C there were several rows of cells and also several cells in one and the same row with an archesporial character. Thus the one archesporial cell is a tapetal cell of the other one. The last produced cells at the top of the ovule have not archesporial structure but are ordinary tapetal cells. The same state of things as the above I have found also in *Quassia*

amara, *Iringia* (fig. 34 G), and others, viz., no pronounced subepidermal arche-sporium, but at once, in very young ovular papilla, as in fig. 33 H, several cells with archesporial structure in the interior of the nucellus. My opinion about the formation of the archesporium in these plants is thus the following. The young ovular papilla grows until it has reached a certain degree of maturity as regards

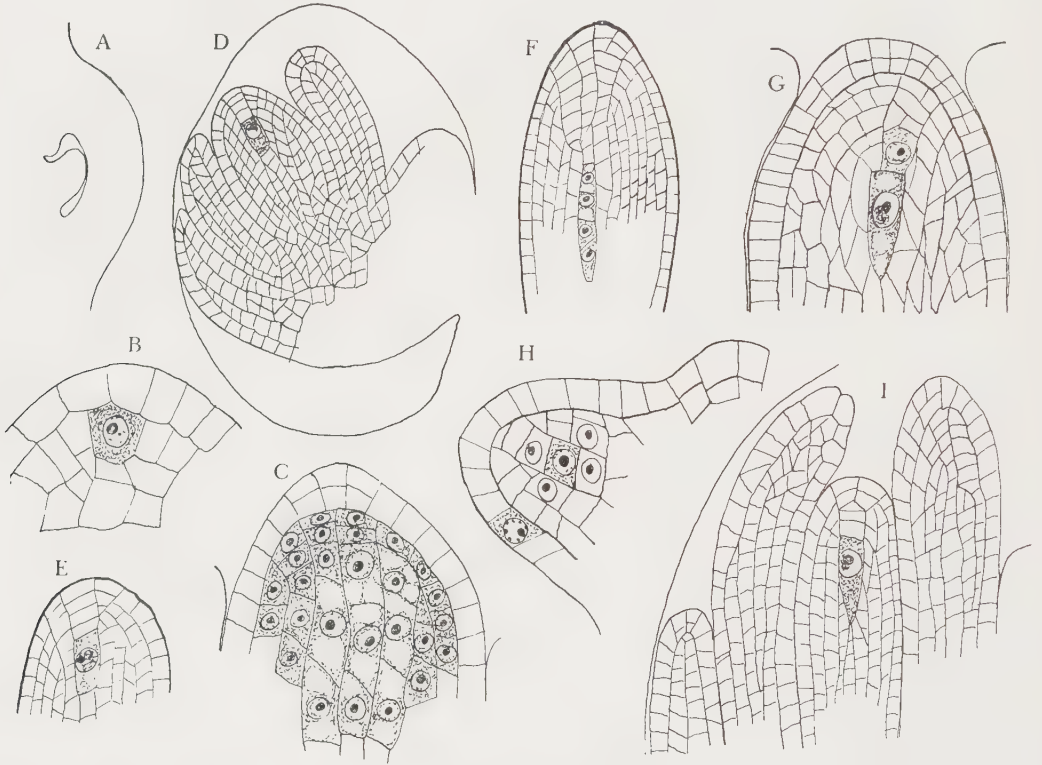


Fig. 33. *A-F Samadera indica*. *A* Longitudinal section through young ovular papilla. $\times 70$. *B* Subepidermal archesporial cell. $\times 600$. *C* Many-celled archesporium. Periclinal division in the epidermis. $\times 485$. *D* Embryo sac mother cell under two tapetal cells and one cap cell. Integuments. $\times 185$. *E-F* Consecutive sections, in the one an E. M. C., in the other a tetrad under seven strata. $\times 300$. *G Samadera mekongensis*. Embryo sac mother cell in synapsis; above, one accessory E. M. C. $\times 485$. *H-I Quassia amara*. *H* Many-celled archesporium. An epidermis cell advanced. The integument arising. $\times 600$. *I* E. M. C. Integuments. $\times 300$.

nutrition. Then one — or more — of the inner cells begins a further development and constitutes the archesporium. Only one cell — seldom more — passes through the heterotypical division. This opinion agrees with that of STENAR (1925, p. 13) as to the formation of the archesporium in *Malvaceae* and in other crassinucellate plants, but he presumes hypodermal origin of the initial cell. Further, one could say that all the cells in the young ovular papilla once had a hypodermal position, so that the difference between the various opinions is but a small one.

Fig. 33 D shows the embryo sac mother cell in *Samadera indica*, under only two parietal cells. The epidermis cells have divided. In this nucellus there were, besides, only one or two advanced cells. Thus it is evident that most of the advanced cells do not develop further. The integuments are seen in the figure. The inner one is about 5-layered, the outer is shorter and thinner. The ovule sinks down to pendulous position, the nucellus grows longitudinally. The mother cell then migrates further into the nucellus, the tapetal cells increasing in number to about six or seven before the reduction division takes place, fig. 33 F. Fig. 33 E is a consecutive section to the former fig., with an accessorial mother cell in synapsis. The accessorial cells seem to stop their development with the diakinesis, as I have not seen more than one tetrad in one and the same nucellus in *Samadera*. Fig. 32 F shows a section of ovary and ovules when the tetrad division is finished. The inner integument is not yet quite closed at the point. The vascular strands end in the placenta but are continued into the chalaza by a rather strong bundle of small, plasmodic cells. The outer integument is still somewhat retarded. The further development of nucellus and integuments is seen in fig. 38 H, at the formation of the embryo sac. I shall here speak only of integument and vascular strand, as the nucellus structure will be described below in connection with the embryo sac. The inner integument has grown up above the nucellus point and formed a rather long, tube-like micropyle. It is strongly swollen at the top, to about double the thickness it has round the nucellus, where it consists of about 5—6 strata. The inner epidermis now obtains another structure, the cells become flattened and their contents are strongly tinged. The outer integument has grown up on a level with the inner one. It is a couple of cell-layers thicker than this but grows thinner at the point. The vascular strand, consisting of about ten spiral vessels, has now grown through the funicle into the chalaza.

Samadera mekongensis agrees in the main points with *indica*. The ovular papilla has, however, at first a basal position, but later on it has the same place as in *indica*. Fig. 33 G shows a large embryo sac mother cell in synapsis plus a parietal cell in further growth. The inner integument in *mekongensis* is somewhat thicker than in *indica*, at the time of the embryo sac about seven cell strata round the nucellus and a little thicker at the point. The outer epidermis of the outer integument begins to grow out, the cells become larger, the nuclei smaller and darker.

The rather small ovular papilla in *Quassia amara* (comp. e. g. figs. 31 K and 33 A) arises at the middle part of the placenta in a rather spacious ovary chamber (fig. 31 K). In the somewhat more advanced papilla the archesporium is to be seen (fig. 33 H), not quite evident as a subepidermal one but as a group of more advanced cells under one or two strata. In the epidermis there was seen a cell with a rather large nucleus in division stage. The integument begins to grow out. Consequently this genus has a many-celled archesporium (see further above), but only seldom have I observed more than one in further development. Fig. 33 I shows a good mother cell in synapsis under three parietal cells plus one cap

cell. The mother cell divides in this position, as is seen in fig. 36 G. In some cases I have observed two tetrads in this species. The nucellus grows long and narrow (fig. 33 I), this form being still more marked in later stages. *Quassia* is bitegmic, the inner integument grows up beforehand, forming the micropyle even before the tetrad division. Later on it becomes tube-like and lengthened. It is

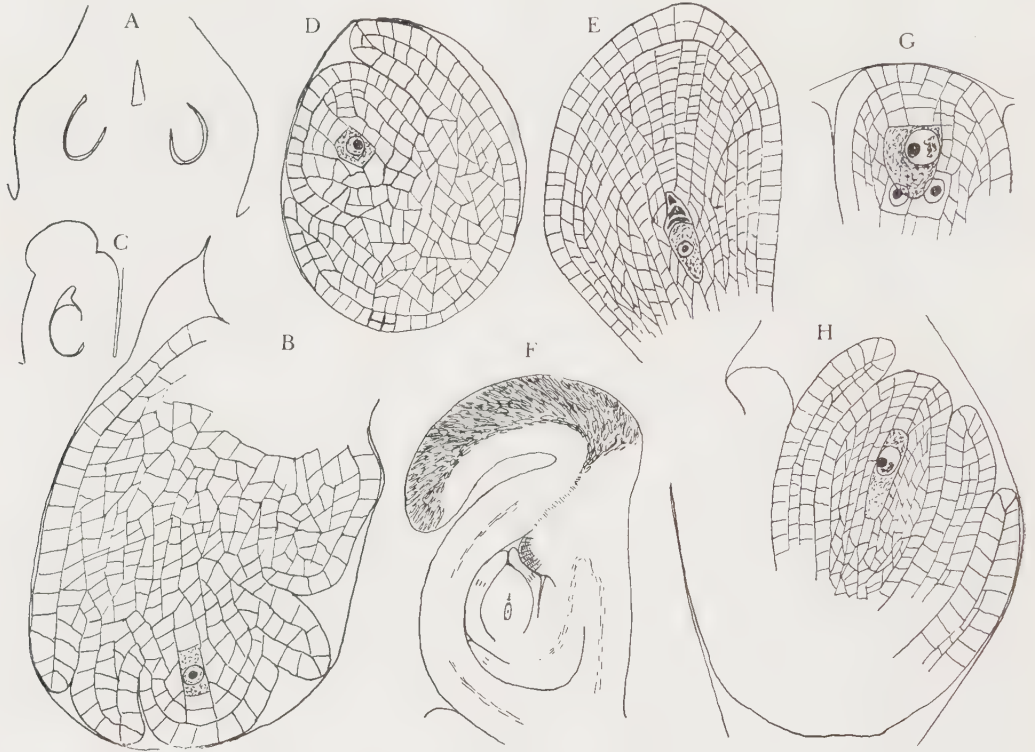


Fig. 34. *A-B Harrisonia Brownii*. *A* The young ovular papillas pendent from the apex of the chambers. $\times 70$. *B* Archeporsial cell, two tapetal cells. The apotropous curve commencing. $\times 400$. *C-F Brucea amarissima*. *C* Young ovary with ovular papilla. $\times 70$. *D* Archeporsial cell, three tapetal cells. Outer integument developing in the epidermis by periclinal division. $\times 300$. *E* Tetrad under 14 tapetal layers. $\times 300$. *F* One free carpel of the gynæceum. Conducting tissue in the stigma. $\times 70$. *G-H Irvingia malayana*. *G* E. M. C., two accessory cells. $\times 485$. *H* E. M. C. Integuments. $\times 300$.

many-layered (fig. 33 I), in later stages the strata are about eight in number. This integument is somewhat thickened at the top. The outer integument is shorter and thinner and exists also at the funicle side in the shape of a more or less marked border.

Young undifferentiated ovular papillas of *Harrisonia Brownii* are seen in fig. 34 A. In this they are fixed apically, and pendent. After some time the archesporium and the integuments are formed, as fig. 34 B shows. At the same time the apotropous curve, occurring in this genus, begins. The funicle thickens, becoming

obturator-like on the inner side. I have not observed more than one archesporial cell in this species. It migrates by the tapetal cell formation down into the nucellus and becomes an embryo sac mother cell. The tapetal cells increase in number to about five in later stages (fig. 37 I), including one or two cap cells. In *Harrisonia* the nucellus gets a more oval form, being at the formation of the embryo sac more or less campylotropous (fig. 37 I), and finally amphitropous (fig. 40 B). Comp. GOEBEL 1923, p. 1724. *Harrisonia* is bitegmie. From the beginning the inner integument is three-layered, the outer two-layered, and this shape they retain, as a rule, during the whole development. The inner dominates also in this species, grows up and forms the micropyle; as a rule, after the division of the mother cell. A later stage is shown in fig. 37 I, at the time of the formation of the embryo sac. On account of the narrow space, smaller than in epitropous species, the inner integument pushes against the placenta and becomes flattened and swollen at the point forming a rather long micropyle. Already in this stage the inner epidermis of it begins to change its structure, in the upper part, the cells being resinous and yellow-coloured. Later on this layer forms the inner stratum of the seed testa (fig. 42 E). The outer integument also gets a similar structure. The outer cells of it increase in size, take on a cubical form, and become plasma-thin, the nuclei being small and dark-coloured (fig. 37 I). This layer as well as the inner stratum of the same integument is later on filled by yellow resin grains and form the outer strata of the seed testa (fig. 42 E). See further as to this below. The outer integument occurs also on the raphe-side (see fig. 37 I). A strong vascular strand is visible in the funicle.

Of *Holacantha* I had no earlier stages than complete embryo sacs. There are two integuments forming the seed testa. See below.

A young, rather thick ovular papilla in *Brucea amarissima* is seen in fig. 34 C. It fills up the chamber almost entirely. A later stage with an embryo sac mother cell under three parietal cells is shown in fig. 34 D. No periclinal division in the epidermis was as yet visible. The inner integument grows up round the nucellus and is three-layered. The origin of the outer one is indicated by periclinal division in two epidermis cells. No many-celled archesporium has been observed in this species. An abundant tapetal cell formation takes place, pushing the E. M. C. far down into the nucellus before the tetrad division begins. Fig. 34 E shows the appearance of the nucellus when the division is finished. On account of the strong growth of the point the nucellus has become pear-shaped. The parietal cells are 14, to which is added one cap stratum. A view of the ovule, and of the whole gynaeceum, at this time, is given in fig. 34 F. The ovule fills up the entire partition. The inner integument has closed above the nucellus. It is 4-layered. The outer one is 3-layered and almost rudimentary at the base of the ovule. A border of it occurs on the raphe-side. The further development in *Brucea* is rather interesting. It is shown in fig. 35 B, at the ripening of the embryo sac. The inner integument is tube-like and lengthened and by pushing against the placenta more or less folded, the micropyle thus being rather long and winding. By a rich

periclinal division the placenta meets the integument and a strong cap formation in the nucellus point, of about five or six strata of cells, aids in filling up the space above the nucellus. The purpose of this cooperation of placenta, integument and nucellus seems to be to form the best possible continuous conducting tissue for the penetrating of the pollen tubes into the embryo sac. The outer integument is still weak; a solid vascular strand goes into chalaza.

The single species of this family, before object for embryological studies, is *Ailanthus glandulosa*. SCHÜRHOFF (1924, p. 732) reports in this species a 1-celled archesporium. No figure accompanies his description. I have not devoted special

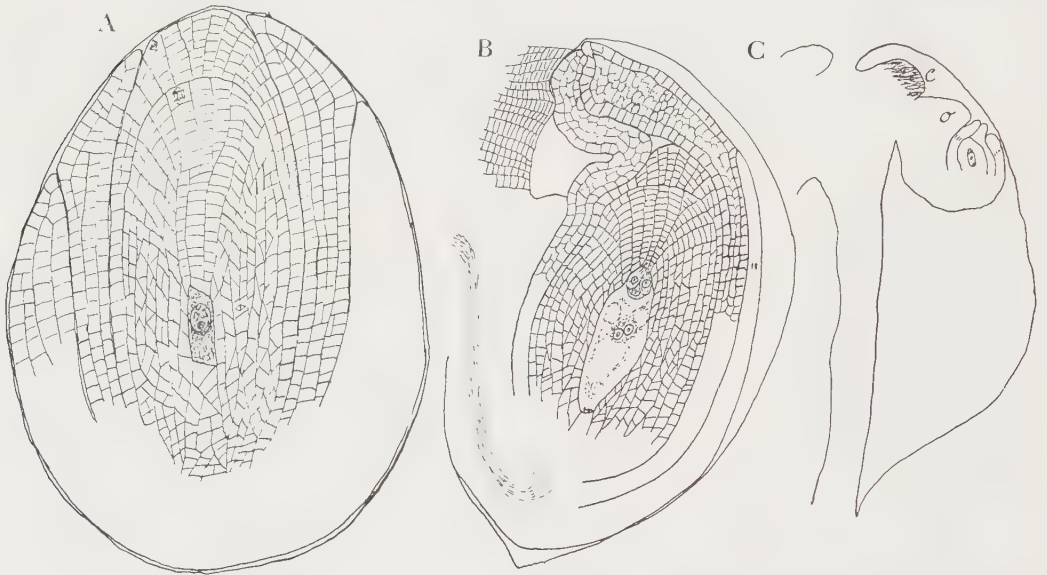


Fig. 35. A *Ailanthus malabarica*. Embryo sac mother cell under 22 tapetal cells plus 7 cap cells. Integuments. $\times 225$. B *Brucea amarissima*. Ovule and placenta at the time of fertilization. See text. $\times 75$. C *Picrodendron baccatum*. Ovary and ovule in later stage. o obturator, c hair cushion. $\times 25$.

attention to the earliest stages. The young ovular papilla depends from the upper part of the chamber and divides later into nucellus and integuments, as is shown in fig. 36 A. A well developed E. M. C. in synapsis is visible under three parietal cells. Periclinal division has begun in the epidermis. At the side of the mother cell there was another advanced cell with a rather large nucleus, wherefore it seems probable that also in this species more than one archesporial cell may sometimes occur, although only one develops further. *Ailanthus* is bitegmic. The inner integument is 2—3-layered and forms the micropyle at the time of the tetrad division (fig. 36 B). The outer one becomes somewhat stronger than in most of the species above described. It does not, however, reach the nucellus point (fig. 32 K). An abundant tapetal and cap cell formation sinks the mother cell deep into

the nucellus before the division takes place. In fig. 36 B this is realized under about 13 cell strata of which only a few are cap cells.

A similar massive nucellus occurs in *A. malabarica* and *altissima* (fig. 35 A, 40 D). In fig. 35 A of the former species the mother cell is still undivided under twenty-two parietal plus seven cap cells. The cap was here distinctly limited. The growth of the nucellus top in this genus is rather similar to that of certain genera in *Burseraceae* (see below, fig. 43 K a. o.). The inner integument in *Ailanthus malabarica* is 3—4-layered, somewhat swollen at the point as also in *glandulosa*. The outer one is shorter and weaker as is generally the case in this family.

In one ovule of *A. malabarica* I saw two nucelli (fig. 36 C). In both of them there was a tetrad placed far down into the chalaza under about twenty-five strata of cells. The two nucelli were grown together without any integument between them, but normal integuments enclosed them. In *Ailanthus*, as in other genera, there is a resinous hypostasis in the chalaza.

In the syncarpous, 2-celled ovary of *Irvingia malayana* the ovules arise in the way shown in fig. 31 F, not above the middle of the chambers, as ENGLER notes. The placenta is considerably thickened above the ovules. These soon become bent in epitropous direction. I have not made a close study of their earliest stages but nothing indicates any deviation from the others. That several archesporial cells occur is evident from fig. 34 G, in which a voluminous E. M. C. in synapsis is visible plus two accessory cells. Moreover, several such cells were found in this ovule. Tapetal cells and cap are to be seen in the figure. A later stage is found in fig. 34 H. The epitropous curve is completed and the nucellus has changed its form from short and broad to long and narrow. A rather long mother cell (length 45 microns) is visible under four top layers including the cap. A couple of accessory mother cells occurred. The same state of things was found in the nucellus from which fig. 37 A was drawn, viz. a rather large mother cell plus two accessory ones. The tetrad division takes place in the position of the mother cell given in fig. 34 H, but even under only three strata of cells I have seen a tetrad. Later on the ovule in this species becomes still more lengthened, as is seen in fig. 39 E. The funicle, rather long and thin, is fastened at the basal end of the ovule and in the lower part of the placenta, as the fig. shows. A rather large vascular strand passes through the funicle into chalaza. I here take the opportunity to compare this figure with that of *I. gabonensis* in ENGLER (1931, fig. 187 F). From this latter it is evident that a considerable difference must exist between the two species as to the placentation of the ovule. As is seen in his figure ENGLER locates the fastening of the ovule to the upper part of the chamber at the place where the outer integument is visible on the raphe-side. I had no material of *gabonensis*, but with regard to the agreement which seems to exist between the ovules of the two species, it seems to me probable that ENGLER's figure, as well as his statement in the text as to this species, are in this respect erroneous.

The integuments in *Iringia malayana*, in later stages, are rather thin and weak. The thickness of the nucellus in the stage shown by fig. 39 E is only about five cell layers round the rather long and narrow embryo sac. From chalaza to the sac there passes a strand of long and narrow nutrition-conducting cells.

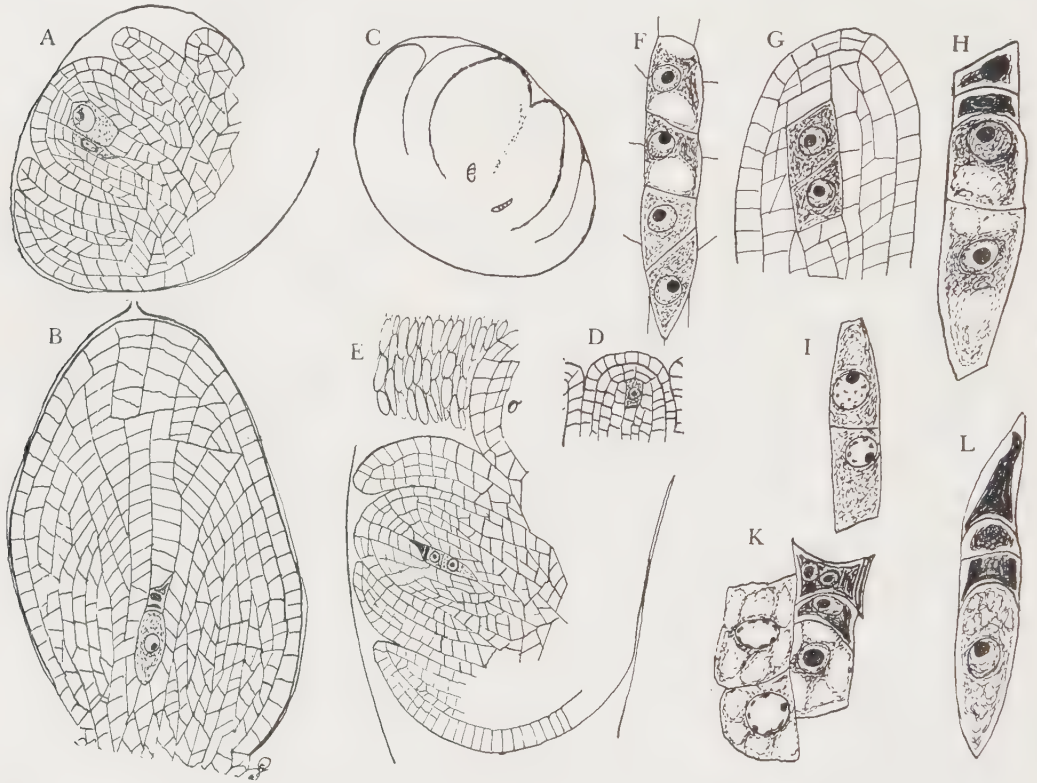


Fig. 36. *A-B Ailanthus glandulosa*. *A* E. M. C., accessory cell, integuments. $\times 185$. *B* 1-nucleate embryo sac with tetrad remains under about 14 strata. Micropyle closed. $\times 300$. *C, I, K Ailanthus malabarica*. *C* Two nucelli in one ovule. $\times 80$. *I* Dyad. $\times 600$. *K* T-tetrad. Large nucellar cells round the tetrad. $\times 830$. *D-E Picrodendron baccatum*. *D* Archegonial cell. $\times 185$. *E* The ovule at the tetrad division. Two tetrad cells advanced. *o* obturator, with hair cushion above it. $\times 185$. *F Samadera indica*. Tetrads. The two upper cells in growth. $\times 900$. *G-H Quassia amara*. *G* Dyad, somewhat acentric. $\times 485$. *H* Tetrads with two cells in growth. $\times 1030$. *L Harrisonia Brownii*. 1-nucleate E. S. with tetrad remains $\times 900$.

Picrodendron, finally, in its syncarpous, 2-celled ovary gives rise to two pendulous ovules in each chamber (fig. 32 E). They are placed on the middle part of the placenta, the point bent upwards in epitropous direction, as fig. 32 B shows. The ovary wall has numerous mucus vesicles. I have not investigated the earliest archesporium stages but only when a couple of tapetal cells had been formed (fig. 36 D). I have not observed more than one archesporial or embryo sac mother cell. Two integuments occur, similar to other *Simarubaceae*. The inner is 4-

layered, somewhat swollen at the point; the outer one is a little thicker than in the majority of species, getting in later stages a thickness of about 5—6 strata. It is of the same length as in other species in this family, since it does not take part in the formation of the micropyle (fig. 35 C). As is evident from fig. 36 E the inner integument in *Picrodendron* does not form the micropyle until the tetrad division has taken place. By further tapetal and cap formation the E. M. C. wanders down into the nucellus and passes through the tetrad division under about 4—5 layers of cells (fig. 36 E). During the nucleus division in the embryo sac the number of strata increases to about 8—10, and then, finally, to 12—15 or, at times, more, during the ripening of the sac. Of these about five belong to the epidermis cap. In *Picrodendron* the nucellus grows broader than in most of the other species, or to about fifteen layers round the embryo sac. It is thus rather massive. Later on the sac absorbs a good deal of the nucellus.

As a summary of the above statements of nucellus, archesporium and integuments in this family the following may be noted. Most of the genera are rather strongly crassinucellate, and bitegmic. Especially *Ailanthus*, *Brucea*, and *Picrodendron* have a massive nucellus. Only *Suriana* is unitegmic. In some genera there was a many-celled archesporium, as in *Samadera*, *Quassia*, and *Irvingia*. Cap formation in the nucellus point is found in all the genera but is not particularly strong. Only in *Ailanthus*, and *Brucea* the cap is somewhat thicker. *Harri-sonia* deviates from other *Simarubaceae* in having an apotropous ovule.

The tetrad division. Formation of the embryo sac.

The tetrad division. In all species of which I have seen the development and division of the mother cell these take place in the normal manner with immediate wall formation, whereas the megaspore development is in this family somewhat variable. Judging from the prophase stages, observed in most of the species investigated, I can say that the division of the mother cell is no doubt a heterotypic one. Synapsis is, as usual, the prophase stage most often observed.

The material of *Suriana maritima* contained no tetrad division stages, but judging from the strongly tinged remnants of cells which I have seen above the embryo sac (e. g. fig. 40 C), the mother cell probably undergoes normal division and then constitutes an embryo sac out of the chalazal megaspore.

Samadera has, as stated above, a many-celled archesporium (fig. 33 C), only one cell, however, seems to undergo heterotypical division. Fig. 36 F (the same as in fig. 33 F) is a regular tetrad in *indica*. The upper cells were larger and also vacuolized, which was not the case with the two lower ones. *S. mekongensis* seems quite to agree with *indica* in its tetrad division.

Fig. 36 G shows a dyad of *Quassia amara*. It had a somewhat acentric position, but was well developed. The cells were the same size. The tapetal cells

were three in number. Regular tetrads have been proved in several cases (fig. 36 H), once or twice two in one and the same nucellus. The development of the megaspores in *Quassia* is rather variable; see below. *Harrisonia Brownii* has also normal tetrad division, as is evident from fig. 36 L. The position of the ovules at this time is seen in fig. 31 B.

Above I have described the rather abundant tapetal and cap cell formation in the genus *Ailanthus* (fig. 35 A and 36 B). Especially *malabarica* has a massive nucellus in which the mother cell was still undivided under more than twenty tapetal cells plus seven cap strata. The division takes place far down in chalaza. A normal tetrad with 13 parietal cells in *glandulosa* is visible in fig. 36 B. A dyad has been observed in *malabarica*, fig. 36 I. The cells were the same size, but the upper had larger nucleus. In the double nucellus, fig. 36 C, of the same species was found a tetrad in each part; the one was a normal row tetrad, the other was T-shaped (fig. 36 K). Further, there was found in chalaza a number of rather large and vacuolized cells with large nuclei, containing some clearly visible chromatin grains. In one nucleus I could count about fifteen grains. Probably these cells are vegetative nucellar ones.

Also in *Brucea amarissima*, *Irvingia malayana*, and *Picrodendron baccatum* normal tetrads have been proved as is shown in the figures 34 E, 37 B-D.

With the exception of the above mentioned case of T-tetrad in *Ailanthus malabarica* no other arrangement of the megaspores than row tetrad has been observed in the material of *Simarubaceae* studied.

The megaspore germination in this family displays several interesting variations, of which the following may be worth mentioning. Thus it has been established that in several genera the micropylar megaspore develops into an embryo sac.

Fig. 36 F is a fine row tetrad of *Samadera indica*, in which the two chalazal cells showed no evident growth, but no degeneration either. The upper cells, however, had manifestly undergone further development. The uppermost cell had a vacuole in each end, the other only one in the lower part. The nuclei were embedded in plasma bridges. This tetrad had thus a tendency to further development of the micropylar megaspores and to abortion of the chalazal ones. In fig. 37 E this development is quite evident. The micropylar cell had here developed into a two-nucleate embryo sac, the next one had also grown out but was degenerating, although the nucleus was still visible. Both the lower spores were disorganized. I have in this species seen the same state of things in several ovules but also traces of reverse development, as in fig. 37 F, where no tetrad remnants were visible below the 2-nucleate sac but only above the latter. It may be noted that the absorbing of the dying megaspores in fig. 37 E takes place in the same order as is the rule when the chalazal cell develops into an embryo sac, i. e. commences with the farthestmost cell and proceeds towards the vital one. This fact seems here rather peculiar as the nutriment is supplied from the chalazal side. A special tissue strand of long, narrow cells leads from chalaza up to the megaspores (fig. 38 H). Moreover, the dying of the megaspores in plants is, generally,

a peculiar and interesting question, hitherto unexplained. Several authors have spoken of the problem, e. g. SCHNARF (1929, p. 115 a. f.). A very common fact, known to all embryologists, is that the first cells to die in the vicinity of a vital megaspore, are its sister cells (e. g. fig. 36 B). One might ask: why are not the cells lying immediately on the other sides of this megaspore as soon absorbed. It seems probable that the walls between the megaspores and the vegetative nucellar cells are more resistant and less permeable than the walls between the spores. The four megaspores no doubt form, to a certain degree, a completed unity. Another question in this connection is the necro-hormon theory of HABERLANDT (1921, 1922, a. o.), viz. that dying cells should have a stimulating effect on surviving ones. Without going into this problem I only refer to the authors mentioned.

The development of the micropylar megaspore into embryo sac is not a common phenomenon in plants. The best known cases occur in *Oenotheraceae*, wherefore these have given rise to a special embryo sac type, named the »*Oenothera* type». TÄCKHOLM (1914, 1915) studied many such cases in this family. SCHNARF (1931) has a detailed list of literature on investigations of this kind, to which I refer. Also in other parts of the system such cases of embryo sac development have been found, e. g. in *Rosaceae*. TÄCKHOLM (1923, p. 219) notes and draws several proved cases of development of the upper tetrad cell in the group *Caninae* of this family. See also SCHNARF.

Samadera mekongensis seems to have a macrospore and embryo sac development similar to *indica*. The many-nucleate nucellus cells which occur in *indica*, and are mentioned further below, exist also in *mekongensis*.

A rather variable megaspore germination was observed also in *Quassia amara*. I have seen typical tetrads with normal chalazal macrospore development (fig. 36 H, 37 G) but also an equally evident formation of an E. S. out of the micropylar tetrad cell, as in fig. 37 H. In this tetrad also the chalazal cell seems to have undergone a certain growth. Moreover, I have in this species several times observed two tetrads in one and the same nucellus. In such a case the one tetrad had the two chalazal cells advanced, something like fig. 36 H, in the other the nethermost cell but one was the largest.

A variable megaspore development has been described in many families from different parts of the system; see PALM (1915, p. 138 a. f.) and SCHNARF (1929, p. 108 a. f.). From the lists of families, given by the authors mentioned, it is evident, as SCHNARF points out (l. c.), that certain Orders, as *Terebinthales* to which *Simarubaceae* belongs, are not represented. Probably this depends upon this Order having hitherto been only slightly investigated. PALM (l. c.) calls attention to the fact that of the cases with variable megaspore development known to him about 75 per cent have many-celled archesporium. As stated above, *Quassia*, and *Samadera* belong to this kind, too. I agree with the author mentioned in his idea that a several-celled archesporium, as also a few-celled one, is a nutrition fund of great importance. »Die entwicklungsfähige Tetrade, bezw. Tetraden,

kommen somit in ein Nahrungsgewebe eingebettet zu liegen, wodurch, gleichwertige Ausbildung ihrer einzelnen Makrosporen vorausgesetzt, jede Makrospore ebenso grosse Chancen der Keimung wie die anderen haben dürfte.» (PALM, l. c.) Also JACOBSSON-STIASNY (1914, 1918, p. 8) considers that favourable nutrition conditions play an important rôle for the megaspore germination.

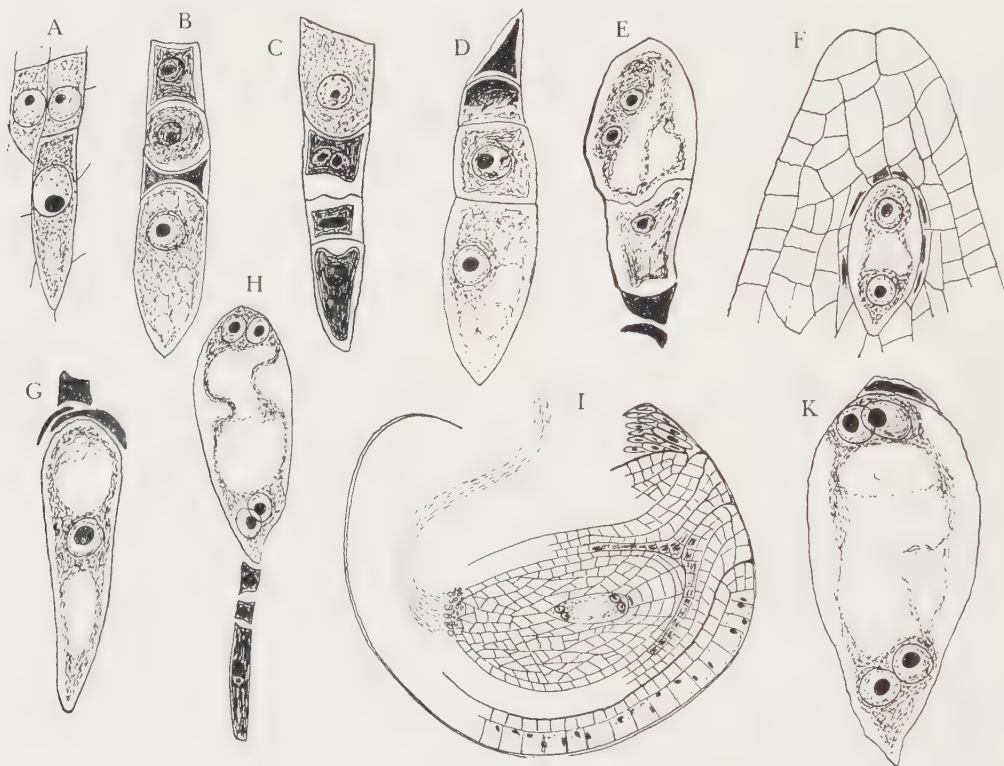


Fig. 37. A-C *Irvingia malayana*. A Embryo sac mother cell with two accessory cells. $\times 600$. B Normal megaspore development. $\times 900$. C Reverse megaspore germination. One of the degenerating megaspores with divided nucleus. $\times 830$. D *Picrodendron baccatum*. Tetrad. The nethermost cell developing into E. S. The next megaspore in growth. $\times 900$. E-F *Samadera indica*. E The micropylar megaspore developing into E. S. The next cell in growth. $\times 830$. F 2-nucleate E. S., probably out of the chalazal megaspore; tetrad remnants above. $\times 485$. G-H *Quassia amara*. G 1-nucleate embryo sac; normal type. $\times 1030$. H 4-nucleate E. S., out of the micropylar megaspore. $\times 600$. I-K *Harrisonia Brownii*. I The ovule at the formation of the E. S. $\times 185$. K 4-nucleate E. S., the same as in the former fig. $\times 900$.

Harrisonia Brownii, and *Brucea amarissima* have shown no case of megaspore development deviating from the normal one (fig. 36 L, 34 E). *Ailanthus glandulosa* had, besides normal cases (fig. 36 B), also a tetrad with the uppermost cell but one developing into an embryo sac (fig. 38 C). In the above mentioned T-tetrad, observed in *A. malabarica* (fig. 36 K) normal germination occurred. The chalazal cell was vacuolized, evidently having been in growth, the upper ones

were disorganized, although the nuclei were still visible. Of *A. altissima* I have not studied earlier stages than after fecundation.

Irvingia malayana had the same variable development as *Samadera* and *Quassia amara*. Fig. 37 B thus shows a tetrad in which normal germination takes place. The lowest cell develops into a 1-nucleate embryo sac, the nearest cell is a disorganized, black-coloured remnant, the two upper ones show signs of degeneration, although the nuclei are still visible. Fig. 37 C, on the other hand, is an example of a tetrad with clearly reverse conditions, as the micropylar cell alone had been in growth, whereas the others were strongly tinged and degenerating. The nuclei were, however, visible as black bodies. In the uppermost cell but one this had even divided. Such cases of another tetrad cell than the E. S. having divided its nucleus are not seldom observed in plants. The greatest interest is then afforded by such tetrads as the above, viz. when the upper cell develops into an embryo sac. TÄCKHOLM (1915, p. 296), for instance, notes a quite similar case in *Jussieuia*, but with the difference that the third cell from the top had divided its nucleus. The same author (1914, p. 231) observed in *Lopezia coronata*, another species developing the uppermost tetrad cell, that the sister cells divided their nuclei. Other plants displaying the same condition are mentioned in the literature.

Picrodendron baccatum, finally, generally develops the chalazal macrospore into embryo sac. I was able to establish this in several nucelli. Fig. 37 D is a tetrad in which the lower cell becomes an embryo sac, but the next spore also had germinated. In the tetrad in fig. 38 E we have, however, another state, viz. the nethermost megaspore but one developing into an embryo sac.

Formation of the embryo sac. The dominating and remaining macrospore grows in connection with vacuolization, as several figs. show, e. g. of *Quassia amara* (fig. 37 G). In this rather normal sac which was broadest at the top and became continuously thinner downwards, the nucleus lay in a broad plasma bridge in the middle part. A large vacuole occurred in the upper and lower parts of the cell. Other primary embryo sacs are visible e. g. in fig. 36 H, L, and fig. 37 B, D. The nuclei are, as usual, placed in the middle or upper part of the sac. When growth is finished the nucleus divides, whereupon normal polarity takes place. The nuclei are embedded in plasma at both ends, and a large vacuole occupies the middle part, as usual. Such a normal 2-nucleate embryo sac has been observed e. g. in *Samadera indica* (fig. 37 F). The sac drawn in fig. 37 E of the same species seems to have just divided its nucleus so that polarity had not yet occurred. The sacs in *Samadera* lie high up at the nucellus points, as in fig. 38 H, under only one or two tapetal cells plus ditto cap cells. As to the nucellus structure visible in the figure, see below.

The embryo sac grows further, whereupon the two nuclei divide. Four-nucleate sacs have been observed in several species, fig. 37 H-K, 38 A-B, E. In all these the nuclei lie in plasma portions at the poles connected by a sack of wall plasma. A large vacuole occupies the centre, at times also a smaller one is found under the lower nucleus group (fig. 38 A-B). The division of the nuclei is

synchronous at both ends, as far as I have been able to show. The position of the nuclei is, in the sacs mentioned, rather equal. In the upper group they lie abreast, as the sac here is rather wide; at the chalazal end they accomodate themselves to the space: if the sac is broad, the nuclei lie abreast, if narrow, they lie one above the other, as in fig. 38 E. In *Ailanthus* the nuclei seem often to have a transverse position also at the lower end. A vacuole occurred under the chalazal nucleus group in *glandulosa* and *malabarica*. This was not the case in other genera.

After further increase in size of the sac the nuclei divide the third time, now also, in the cases observed, synchronously. The result is an 8-nucleate embryo sac with a group of four nuclei at each end separated by a vacuole. Such undifferentiated sacs have been seen in some species. Fig. 38 C is a sac of *Ailanthus glandulosa* in which no cell formation had yet taken place; the polar nuclei, however, had come into contact. SCHÜRHOFF (1924) reports also an 8-nucleate embryo sac in this species. Also in *Samadera indica*, and *Irvingia malayana* I have seen the nuclei more or less collected in groups. Fig. 38 F shows a sac of *Picrodendron baccatum* in which the polar nuclei had begun wandering. The other nuclei were still embedded in homogeneous plasma at each end. In other sacs of this species the four nuclei were still quite collected.

After cell formation we have at the upper end of the sac an egg apparatus, in the lower part an antipodal one, further two free polar nuclei which meet as usual, whereupon the sac is mature for fertilization. Some ready built sacs of this kind may be noted. Fig. 38 D is a ripe sac in *Ailanthus glandulosa*. First we may note the approximate increase in size after the 4-nucleate stage seen in fig. 38 B and drawn on the same scale. The egg apparatus seems on the whole normal as to the position of the nuclei and the vacuolization. In one synergid the nucleus lay rather far down. Point structure occurred. The egg cell hung below the synergids with its sack-like part. There were three antipodals, two abreast above the third which was placed at the point. The polar nuclei had contact in the middle of the sac.

Picrodendron baccatum showed fine embryo sacs of the type visible in fig. 38 G. First we may compare the size of this sac with that of the 8-nucleate one in fig. 38 F. The mature sac has grown out to about double in length and breadth. In most of the sacs observed in this species the synergid nuclei had the position shown in the figure, viz. in the middle part of the cells. Vacuoles always occurred in the basal part. The egg cell was quite normal, as also the antipodals, of which one was placed at the point and the other abreast above. The position of the polar nuclei varied, but often they had contact below the egg apparatus, as in fig. 38 G. I always found a green-coloured thread structure in the synergids. The mature embryo sac in *Picrodendron* was placed far down in chalaza with a massive tissue of about fifteen strata above it. No fertilization or embryo formation occurred in the material of this species studied. In waiting for fertilization the embryo sacs begin to hypertrophy, growing in length as well as in breadth, finally occupying

a great part of the nucellus. The contents degenerate with the exception of the polar nuclei which fuse into a primary endosperm nucleus. But I have in no case seen this divided give rise to an endosperm. In later stages the primary endosperm nucleus was the single body that remained in the embryo sac, whereas the egg and antipodal apparatus were quite absorbed. The nucellus cells in such

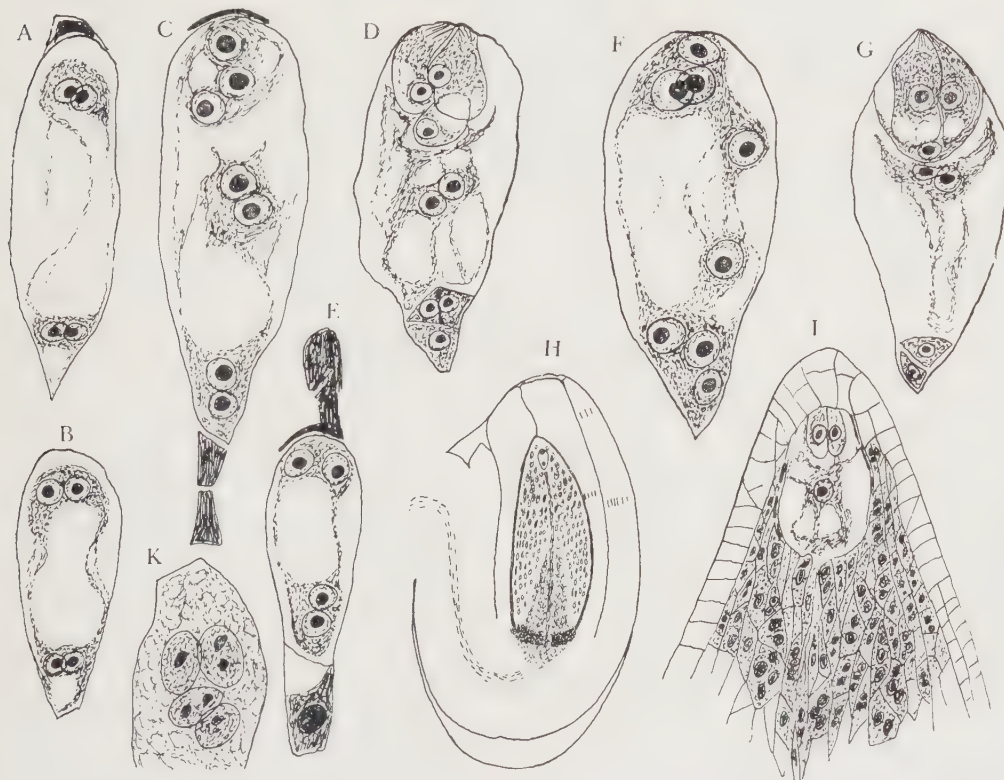


Fig. 38. *A* *Ailanthus malabarica*. 4-nucleate embryo sac with tetrad remnants. $\times 600$. *B-D* *Ailanthus glandulosa*. *B* 4-nucleate E. S. $\times 400$. *C* 8-nucleate E. S., out of the next uppermost megaspore. One nucleus not drawn. $\times 600$. *D* Mature E. S. $\times 400$. *E-G* *Picrodendron baccatum*. *E* 4-nucleate E. S., out of the next nethermost megaspore. $\times 830$. *F* 8-nucleate E. S.; the polar nuclei in migration. $\times 900$. *G* Ready built E. S.; one antipodal in the next section. $\times 400$. *H-K* *Samadera indica*. *H* The ovule at the formation of the E. S. See the text. $\times 70$. *I* E. S. with primary endosperm nucleus. Many-nucleate nucellus cells. $\times 300$. *K* Nucellus cell with four nuclei. $\times 900$.

unfertilized ovules had very thin contents. The ovaries had, however, grown out considerably, the chambers were large cavities with the ovules placed high up in the upper part, as fig. 35 C shows.

Fig. 39 F is a ripe embryo sac of *Irvingia malayana*. It is long and narrow, as well as the nucellus in this species, and lies high up in the upper part of the ovules, under only a few tapetum strata. The egg apparatus seems rather normal,

the antipodals, three in number, soon become absorbed. The polar nuclei have contact in the centre of the sac. Later on they fuse and form an endosperm.

Fig. 40 C shows a completed but still unfertilized sac in *Suriana maritima*. It had not yet begun the amphitropous curve. The antipodals were almost completely absorbed. The polar nuclei had contact in the centre of the sac. The egg apparatus was rather normal. Point structure was visible.

The *Samadera* species had their mature embryo sacs farthest up under the nucellus point. They absorb all the tapetum cells, so that only the epidermis remains (fig. 38 I). The sacs seem to degenerate, excepting the polar nuclei, whose fusion product was observed (figs. 38 I, 39 I). I had no later stages of this genus at my disposal, so that I cannot say anything about the further development of the embryo sac.

A rather interesting fact observed in *Samadera* is that at the time of the nucleus divisions in the embryo sac the nucellar cells get more than one nucleus. This phenomenon seems to begin in the nucellus point and then extend to the whole nucellus far down into chalaza (fig. 38 H-K). The number of nuclei in each cell varied between one and four. It seems seldom to be more than four. The nuclei often had several nucleoli (fig. 38 K). I have observed that the division of the nuclei is a mitotic one. The cytoplasm in the upper cells was rather dense, in the lower ones thinner. The former had therefore an appearance quite reminiscent of young nucellar embryos such as in the genus *Sarcococca* (fig. 13 D-E). Fig. 38 I shows the upper end of the nucellus with the embryo sac and the cells mentioned in *Samadera indica*. Quite similar in this respect is *mekongensis* also. Unfortunately I cannot now decide whether this genus has nucellar embryony, as no later stages were included in the material. Until further studies have been made on the matter one can make this assumption.

The chalazal structure in *Samadera* is worth mentioning. A hypostasis of small, thick-walled, resinous cells fills the chalaza excepting the central part, where a conductive strand of long, narrow cells runs up through the nucellus to the embryo sac (fig. 38 H). A certain connection seems to exist between the hypostasis and the above-mentioned inner epidermis of the inner integument (see fig.). Inside the chalaza, in a cone-shaped part, the nucellar cells become thick-walled and get degenerated, probably mucous, contents (fig. 38 H). A rather solid vascular strand leads into chalaza. The nucellar structure mentioned has no doubt a conductive task. TÄCKHOLM (1915, p. 323 a. f.) reports a similar structure in the chalaza of *Godetia*, *Clarkia* a. o. *Onagraceae*, and expresses the supposition that this plays the rôle of conducting tissue. It may then be noted that in *Samadera*, as well as in the plants mentioned, the micropylar megaspore develops into embryo sac. This latter in *Samadera* lies farthest up at the point of the ovule, the nutrition thus having a rather long way to pass from the chalaza, which has caused development of a special conducting tissue.

The antipodals in *Samadera* are ephemeral and become early absorbed.

Of *Quassia amara*, *Ailanthus malabarica*, or *Holacantha Emoryi*, no mature embryo sacs occurred in the material studied.

Fig. 35 B shows integuments, nucellus, and embryo sac mature for fertilization in *Brucea amarissima*. A normal egg apparatus occurred, with thread structure in the synergids, and polar nuclei in contact in the centre of the sac. The antipodals were absorbed.

The ripe embryo sac in *Harrisonia Brownii* is broad but rather short, fig. 39 A. The egg cell in the sac drawn was normal, the synergids, however, were filled with small vacuoles. The point structure was rather insignificant. The antipodals were three in number and still rather vital. For their placing, see fig. A large, almost hypertrophied primary endosperm nucleus lay in the middle of the sac. Several such sacs were observed, many sacs had, however, developed further.

The antipodals in this family are three in number. They play but an unimportant rôle and become early absorbed.

Fertilization. Endosperm. Embryo.

About the fertilization in *Simarubaceae* no observation had previously been made.

The conducting tissue. The stigmata have in all species a papillous or palisade-like epidermis. The conducting tissue in the style is somewhat different in different genera. *Harrisonia*, for instance, has in each carpel of the united style an isolated canal covered with a palisade-like, plasmous epidermis (figs. 31 C, 39 B). No communication exists between the canals until at the base of the styles where the carpels are free. Here the stylar canals run out through ventral furrows, as fig. 31 D shows, which furrows lead down into the ovary cells. The furrows have palisade epidermis, too. *Picrodendron* has no stylar canals and thus no ectotrophous conducting tissue in the style. An endotrophous one occurs in the centre of the style (fig. 32 D) in the shape of a rather massive strand of lengthened cells with thick walls, whose central membrane alone was green-coloured, indicating cellulose (fig. 39 K). The cytoplasm in these cells was rather vacuolized, and the nuclei were embedded in a plasma bridge, as the figure shows. *Samadera* has a conducting tissue of the type shown in fig. 39 H. Stylar canal is lacking, a central strand of long and narrow, plasmous cells with rather thin walls passes through the style. *Quassia* (fig. 31 H) and *Irvingia* (fig. 31 G) have a similar conducting strand. *Ailanthus* like the former genera has the styles grown together, but here each carpel has a conducting strand (fig. 32 H) of lengthened, loosened, plasmous cells with thickened walls leading down into the ovaries.

Brucea has the rather thick and long stigmata bent backwards, as is visible in fig. 34 F. Their upper sides consist of a conductive tissue of lengthened cells going obliquely from the surface toward the centre, as the figure shows. This tissue is continued by a small-celled, plasmous one leading down into the ovary cells.

Some species have obturator, formed by periclinal cell division in the funicle, e. g. in earlier stages *Brucea*, fig. 34 F. The obturator in this species is later on levelled, the situation at the time of fertilization being that visible in fig. 35 B. No marked obturator exists, but a vivid periclinal division has thickened the

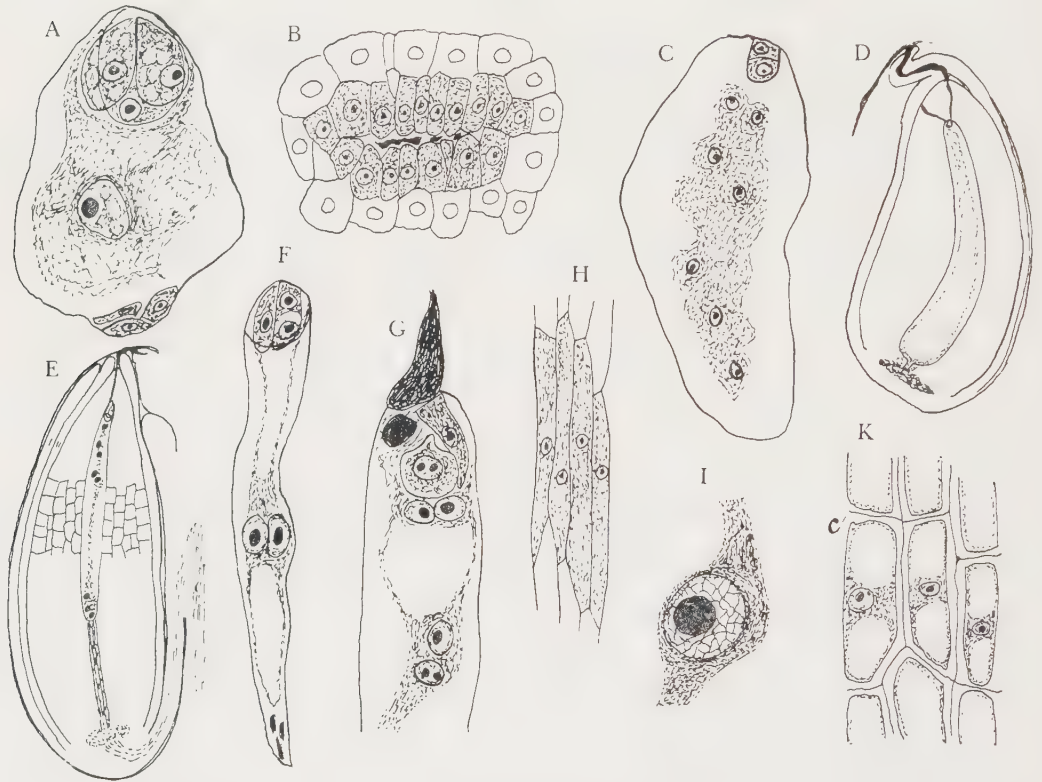


Fig. 39. *A-C Harrisonia Brownii*. *A* Mature embryo sac with definitive endosperm nucleus. $\times 485$. *B* Transverse section through stylar canal with palisade-like epidermis. Pollen tubes visible. $\times 485$. *C* E. S. with 2-celled embryo and 16 endosperm nuclei. $\times 185$. *D Brucea amarissima*. Nucellus and E. S. campylotropously curved. Pollen tubes in micropyle and nucellus. Nuclear endosperm. $\times 10$. *E-G Irvingia malayana*. *E* Ovule at the time of fertilization. Pollen tube in micropyle. 8 endosperm nuclei. $\times 70$. *F* E. S. $\times 400$. *G* Fertilized egg cell; 32 endosperm nuclei in the sac. $\times 600$. *H Samadera mekongensis*. Conducting tissue in the style. $\times 600$. *I Sam. indica*. Primary endosperm nucleus. $\times 900$. *K Picrodendron baccatum*. Conducting tissue; *c* cellulose membrane. $\times 600$.

funicle. At the same time the inner integument becomes lengthened, tube-like. Owing to lack of space somewhat curved at the point and pressed against the placenta, it forms a continuous conducting bridge over to the nucellus. A rather thick nucellus cap fills up the space inside the micropyle. The structure now described has no doubt a conducting task at the time of fertilization. *Irvingia* has also an outgrowth from the placenta on a level with the micropyle, as is seen

in fig. 39 E. NETOLITZKY (1926) reports that this outgrowth arises from the funicle, but this statement is incorrect, as is evident from my figure. The funicle is, at least in *malayana*, directed downwards. The author mentioned has shown that this obturator later on enters the endostom.

Concerning *Picrodendron* FAWCETT and RENDLE (1917, p. 269) notice that this has »a reddish-brown cushion-like outgrowth (obturator) springing from the placenta just above the insertion of the pair of ovules and closely roofing over the two micropyles. The obturator does not develop with the growth of the seed but becomes withered.» This statement I can on the whole confirm. But as is seen in my figs. 32 B and 36 E we must here distinguish between two different things. A real and strongly marked obturator exists, but above this we have the »cushion-like outgrowth» mentioned by the authors, consisting of a thick and long pilosity on the placenta. It is this hair cushion that roofs over the micropyle, as fig. 32 B shows. Thus this cushion does not belong to the real obturator. The hairs are long cell threads (fig. 36 E). Later on they become filled with resin grains, and then the organ gets a reddish-brown colour. The statement of FAWCETT and RENDLE that the obturator later on becomes withered is partly incorrect, as it is the hair cushion that withers whilst the obturator remains, as is evident from fig. 35 C.

Fertilization. Pollen tubes in style, or ovule have been observed in the following species: *Harrisonia Brownii*, *Irvingia malayana*, *Ailanthus glandulosa*, and *altissima*, and *Brucea amarissima*.

I have spent much time searching the route of the pollen tubes in *Harrisonia*. The position of the ovules is such that one might suspect porogamy, or chalazogamy, or both (figs. 37 I, 40 B). I am not quite sure about this matter, but I believe the last mentioned to be the case. The tubes are very delicate and thus difficult to follow; in the style, however, they were quite evident (figs. 31 B, 39 B). They follow the styler canals down into the ovary chambers, then going ectotropously round the funicle they pass into the micropyle. It is, however, possible that the tubes at times have an endotropous course in the placenta, and then they pass through the chalaza up to the embryo sac. Future studies may decide this.

Fig. 39 E shows a pollen tube in the micropyle in *Irvingia malayana*. The egg was probably fertilized; the sac contained eight endosperm nuclei. Fig. 39 G is another case in the same species. Judging by the two nucleoli in the egg nucleus this was fertilized. The sac contained 32 free endosperm nuclei. *Irvingia* thus has porogamy.

The course of the pollen tube in *Ailanthus* appeared clearly in the preparations. The figures 32 K, 40 A, D show the course. In fig. 32 K this is partly drawn schematic in stigma and style. The tube passes through the conductive tissue in the style straight into the micropyle. In fig. 40 A the tube was continuously visible from the embryo sac out through the micropyle, where it was somewhat swollen, and further through the wing-like ovary border following the conducting tissue. The same course is taken in *altissima*, fig. 40 D. I saw it creeping ectotropously on the placenta in the manner shown in the figure. In *Brucea* I saw one tube

passing from the style through the winding micropyle into the nucellus point, but one tube seemed to have entered the nucellus from the side, as fig. 39 D shows. The egg cell was probably fertilized but was undivided, evidently abortive. In other sacs there were embryos, and endosperm (fig. 41 F-G).



Fig. 40. *A* *Ailanthus glandulosa*. Pollen tube in micropyle and nucellus; 2-celled embryo; nuclear endosperm. $\times 75$. *B* *Harrisonia Brownii*. Later campylotropous stage of the ovule with nuclear endosperm in the E. S. The chalazal end directed upwards. One ovule rudimentary. $\times 25$. *C* *Suriana maritima*. Mature E. S. The antipodals in absorption. $\times 300$. *D-E* *Ailanthus altissima*. *D* Ovule at the time of fertilization. Pollen tube. Nuclear endosperm. $\times 25$. *E* Upper end of the E. S. with 2-celled embryo and nuclear endosperm (the same sac as in the former fig.). $\times 600$.

I have not seen the sperm nuclei, or the double fertilization, but there is no reason for doubting it.

The endosperm in *Simarubaceae* is nuclear, as was noticed above. Attention may be called to the following. In *Suriana maritima* the endosperm is of some

interest. At the formation of the embryo and endosperm the ovule and the sac become amphitropously curved, as can be seen in fig. 41 A. The sac reaches through the whole nucellus down into the chalaza and is there prolonged into a narrow tip which passes through the hypostasis. Into this point the endosperm enters. *Suriana* has thus an endosperm haustorium in the chalaza of the type previously established in several plants. In the young haustorium seen in fig. 41 A only one or two endosperm nuclei were found. In the other part of the sac numerous nuclei occurred, and also a young embryo. A later stage is seen in fig. 41 D. The ovule is now strongly curved. A somewhat more developed embryo occurred in the top of the sac. The endosperm was cellular in the greater part of the sac, in the chalazal end and in the haustorium, however, it was still nuclear. Below the hypostasis the haustorium was widened, sac-like, and only a narrow passage through the former connected the haustorium with the embryo sac. A number of nuclei had wandered into the haustorium. Fig. 41 B is a stronger magnification of the organ at this time. Some nuclei are just going through the passage and seem rather normal. The nuclei down in the haustorium, however, which have probably been there for some time, are hypertrophied, the nucleoli divided into small grains, and the cytoplasm thin. The cells round the haustorium seem to be disintegrated and absorbed. The haustorium is evidently a typical nutriment-collecting organ for the embryo sac. I had no later stages in the material, so that I cannot say whether the endosperm in the chalazal part of the embryo sac and in the haustorium ever becomes cellular. It may be assumed that the nuclear state remains as long as possible, as this probably renders the best service in gathering nutriment. Otherwise the endosperm would probably have become cellular here at the same time as in other parts of the embryo sac.

From the literature the following cases may be noted similar to the above in *Suriana*, viz. nuclear endosperm haustoria in chalaza. DAHLGREN (1916, p. 65, fig. 112) describes and draws a tip-like nuclear endosperm haustorium in chalaza in *Plumbagella micrantha*. In this, however, cell formation took place at the same time as in other parts of the embryo sac. The cells in the haustorium did not deviate from other endosperm cells. WOODCOCK (1914, p. 457) reports and draws a quite similar organ in *Polygonum persicaria*, and other species. Here the nuclear stage persisted for a long time in the haustorium. BILLINGS (1901, p. 284) notices a long, tiplike, nuclear, chalazal haustorium in *Leptosiphon androsace*. This author, too, saw that adjacent tissues become mucous and absorbed. *Brucea amarissima* has also an endosperm tip in chalaza (see below).

In many cases authors report an agglomeration of endosperm nuclei in the chalazal part of the embryo sac but without any appendix below the hypostasis as in *Suriana*. Such »basal apparatus» TÄCKHOLM (1915, p. 301), for instance, describes in *Onagraceae*, and HÅKANSSON (1921, p. 220) in *Schizocapsa plantaginea*. Also in *Onagraceae* the nuclei were enlarged and irregular in shape. The wall formation had not yet taken place in the latest stages observed by this author. The basal apparatus of the endosperm is considered to be a haustorium. SCHNARF (1929,

p. 361) has a list of several cases of endosperm of this kind. Certain authors consider the enlargement of the nuclei as a sign of degeneration, e. g. JACOBSSON-STIASNY (1914, p. 17) who writes: »Andererseits erscheint eine Hypertrophie der Kerne wohl als eine durch den starken Nahrungsstrom bedingte Degenerationserscheinung, kann aber nicht als notwendiges Kennzeichen eines Haustoriums aufgestellt werden«. No doubt, however, such haustoria as in *Suriana* purpose to gather nutriment for the embryo sac.

In *Samadera indica* I have seen only the fusion product of the polar nuclei, viz. the primary endosperm nucleus (figs. 38 I, 39 I), but no later stages, or division of this. All nucellar tissue was at this time absorbed at the point, so that only the epidermis remained above the embryo sac as in fig. 38 I. The sacs seemed to degenerate, the polar nuclei and the primary endosperm nucleus were, however, vital. The nucleus drawn in fig. 39 I had a fine linin net and a large nucleolus of about six microns in size.

Fig. 39 A shows a large primary endosperm nucleus in *Harrisonia Brownii*. Later on it divides and gives rise to a nuclear endosperm. Fig. 39 C is a drawing of an embryo sac containing 16 free endosperm nuclei rather equally spread in the sac. Fig. 40 B is a later stage with 64 nuclei, half the number of which was collected in a plasmous basal apparatus in the chalaza, of the same sort as mentioned above. The nuclei were, as is often the case, somewhat larger here than in the upper part of the sac. A yellow-coloured, rather massive, resinous hypostasis filled the chalaza, from which a conducting bundle of lengthened cells passed up to the embryo sac. Also the lower part of the nucellus begins to be resinous. As the inner layer of the inner integument, too, in this species is now totally resinous and connected in the chalaza with the hypostasis, as fig. 40 B shows, the whole nucellus at this time is enclosed by a resinous tissue.

Of *Holacantha Emoryi* I had only cellular endosperm in the material. It was of the same shape in the whole embryo sac (fig. 42 B). *Bucea amarissima* has nuclear endosperm and basal apparatus of the same type as mentioned above, viz. the embryo sac at the chalazal end is lengthened into a tip-like, plasma-filled point in the manner shown in fig. 41 G. In this tip there were four endosperm nuclei. The point grows into the hypostasis but does not go through this as in *Suriana*. The bottom of the embryo sac was moreover covered with a plasma stratum lying close to the wall and containing about twenty endosperm nuclei. At the side walls the plasma sack did not fit tight to the wall. The nuclei in this sack were more spread and also smaller in size than in the basal part. Fig. 41 F is drawn from the upper end of the embryo sac. The nuclei had here 1—3 nucleoli. In this species probably thousands of nuclei are formed in the endosperm before the cell formation begins. The hypostasis consists of small, thick-walled cells. The nucellus is at this time campylotropously curved in *Bucea* (fig. 39 D).

SCHÜRHOFF (1926, p. 587) reports nuclear endosperm in *Ailanthus glandulosa*, and this statement I can confirm. *A. altissima* also has nuclear endosperm. Fig. 40 A is a drawing from the upper end of an embryo sac in *glandulosa* containing

numerous endosperm nuclei, and fig. 40 E shows the same state of things in the upper part of a sac in *altissima*. Here the nuclei had one or several nucleoli. The whole ovule with embryo sac of the same species is seen in fig. 40 D. The sac in *Ailanthus* at this time goes through the whole nucellus down into the chalaza. The ovule becomes broad and flattened, as also later on the seed, and the embryo sac gets the same shape, somewhat widened in the basal part. A large number



Fig. 41. *A-E Suriana maritima*. *A*. An amphitropous ovule with embryo and nuclear endosperm. Young haustorium in chalaza. $\times 70$. *C* Higher magnification of the embryo in the former fig. $\times 485$. *D* Later stage. The haustorium sack-like. The endosperm still nuclear in chalaza and haustorium. $\times 70$. *B* Higher magnification of the haustorium in fig. *D*. $\times 300$. *E* Horse-shoe-shaped mature embryo. $\times 15$. *F-G Brucea amarissima*. Upper and lower ends of *E. S.* with embryo and nuclear endosperm. *F* $\times 300$, *G* $\times 185$. As to the cavity below the embryo, see the text.

of endosperm nuclei occurs in these sacs. Numbers of them are accumulated in the lower part as a basal apparatus, but also in the upper and narrower part of the sac the nuclei are somewhat collected. In the middle part there occurs a thinner stratum of wall plasma with more spread nuclei. No tip-like point in chalaza seems to arise in this genus. A broad, flattened hypostasis occurs in chalaza (fig. 40 D).

Figure 39 F shows the long, narrow embryo sac in *Irvingia malayana*. The

polar nuclei meet in the centre of the sac. After fusion the primary endosperm nucleus divides. The two nuclei thus arisen wander one to either end of the sac where each gives rise to a group of endosperm nuclei. The sac still long and narrow becomes lengthened through the greater part of the nucellus, as is shown in fig. 39 E. There were eight endosperm nuclei in this sac, three in the lower, and five in the upper group. The two groups were connected by a thin plasma veil. A conducting strand of long, narrow cells passes from chalaza to the lower end of the embryo sac. The ovule is fastened at the placenta by a rather thin funicle through which a vascular bundle leads into the chalaza. A pollen tube entering the micropyle and the embryo sac, and a probably fertilized egg cell were visible in this ovule. Fig. 39 G is drawn from a fertilized sac containing 32 endosperm nuclei. I saw also in this species sacs with 4 and 16 nuclei.

Of *Quassia* and *Picrodendron* no endosperm and embryo stages were found in the material studied.

The embryo. Embryos were found in several species. Fig. 41 C shows a young one in *Suriana maritima*, drawn from the same embryo sac as in fig. 41 A. Numerous endosperm nuclei had already arisen. The embryo contained four cells. No doubt the primary endosperm nucleus in this species divides somewhat earlier than the egg cell. This latter had in the sac mentioned divided by a transverse wall into one basal and one apical cell which latter had divided again transversely and then by a longitudinal wall into two cells. A more advanced stage is visible in fig. 41 D. The endosperm was mentioned above. A mature embryo is drawn in fig. 41 E. It has now horse-shoe shape and a rather long and thick hypocotyl.

Also in *Harrisonia Brownii* the egg cell divides transversely, fig. 39 C. As in this embryo sac only 16 endosperm nuclei occurred, one may assume that the egg cell and the first endosperm nucleus had divided at about the same time. As is seen in this fig. and in fig. 40 B, the embryo sac and ovule at this time get a campylotropous form. Thus the embryo by further growth gets the shape shown in fig. 42 F, which is drawn from a maturing seed. One cotyledon in this embryo was folded or deformed. The hypocotyl in this species is short, the cotyledons rather long. As is seen in fig. 40 B, all the four ovules in the ovary (fig. 31 E) do not reach full development but some of them abort. In this ovary only one or two seemed to have been in further growth. The rudimentary, abortive ovules, however, develop a mature embryo sac with some endosperm nuclei, but I have never seen any fertilization or embryo in them.

A young embryo in *Holacantha Emoryi* is visible in fig. 42 B. A short and thick hypocotyl and round and thick cotyledons occur. The endosperm is at this time quite cellular. Also in *Bucea amarissima* young embryos were observed, as in fig. 41 F. This embryo had about 13 cells. Longitudinal walls had already been formed in the three apical embryo layers. The suspensor cell was still undivided. A rather interesting fact appears in this figure, and I observed the same matter in all other embryo sacs of this species containing an embryo, viz. the traces of the fixing and the contraction of the cytoplasm by the preserving fluid. When the fixing fluid pene-

trated into the embryo sac, the vital cytoplasm was lying close by the wall enclosing also the embryo. Then the plasma sac drew back from the wall, while the embryo, fastened at the wall, left an evident and equiform cavity in the plasma sac, as the fig. shows. The plasma had been »fixed» in its original situation round the embryo.

In *Ailanthus glandulosa* as well as in *altissima* I observed embryos in the 2-celled stage, figs. 40 A and D-E. The egg divides by a transverse wall in both species, and evidently later than the endosperm nucleus, as in these sacs there was already a great number of endosperm nuclei. Later embryo stages were not included in the material of *Ailanthus*.

Fertilized egg cells were observed in *Irvingia malayana* but no later stages (fig. 39 G). *Alvaradoa amorphoides* has long, narrow seeds and ditto embryos with rather short hypocotyl and long cotyledons (fig. 42 A).

Concerning the possible nucellar embryony in *Samadera*, see above.

The seed.

The seed coat in this family, as a rule, is thin and weak. The micropyle is formed by the inner integument, whereas the outer is short and seems never to reach the point, fig. 40 A-B, D. NETOLITZKY (1926) reports that in *Irvingia* the outer integument consists of three, the inner of four layers, but in *malayana*, at least, the rule is in the former two, in the latter three layers. In *Suriana* there is only one integument. Fig. 42 L shows the seed coat in this species. A thin cuticle covers the nucellus, another seems to occur between endosperm and nucellus. The seed coat consists of the rather thick outer epidermis, with large, green-coloured cells, plus some strata of thin cells. The embryo cells contain plenty of round black drops, probably oil. The same is the case with the embryo in *Harrisonia Brownii*, but not with those of *Holacantha*, or *Alvaradoa*, which seem to have rather thin contents. In *Alvaradoa* the rather thin seed coat consists in the main of the resinous epidermis of the outer integument. The inner epidermis of the inner integument is a thin resinous membrane (fig. 42 A). The seed coat in *Harrisonia* is seen in fig. 42 E. It consists of the resinous inner epidermis of the inner integument, further of plasma-thin, large cells which later become pressed together, and outmost of the outer integument in two layers of cells with resin grains. A cuticle covers the nucellus.

The endosperm in this family contains little or no reserve nutriment. In the embryo there occur, however, oil and aleuron grains. See further NETOLITZKY (1926), and ENGLER (1931).

Pollen development.

SCHÜRHOFF (1924) reports as to *Ailanthus glandulosa* that the anthers in the bisexual specimens show no archesporium but consist of only vegetative cells and are thus to be regarded as staminodia. I have also examined these flowers

and must state that the above report is not quite correct. One must admit that in very young stages there exists a normal archesporium in the anthers with the usual appearance of such a one, viz. plasmodic cells, and larger nuclei and nucleoli than in other cells. But at this point the development seems to stop. No heterotypic prophase stages were observed; the tissue is somewhat later quite homo-

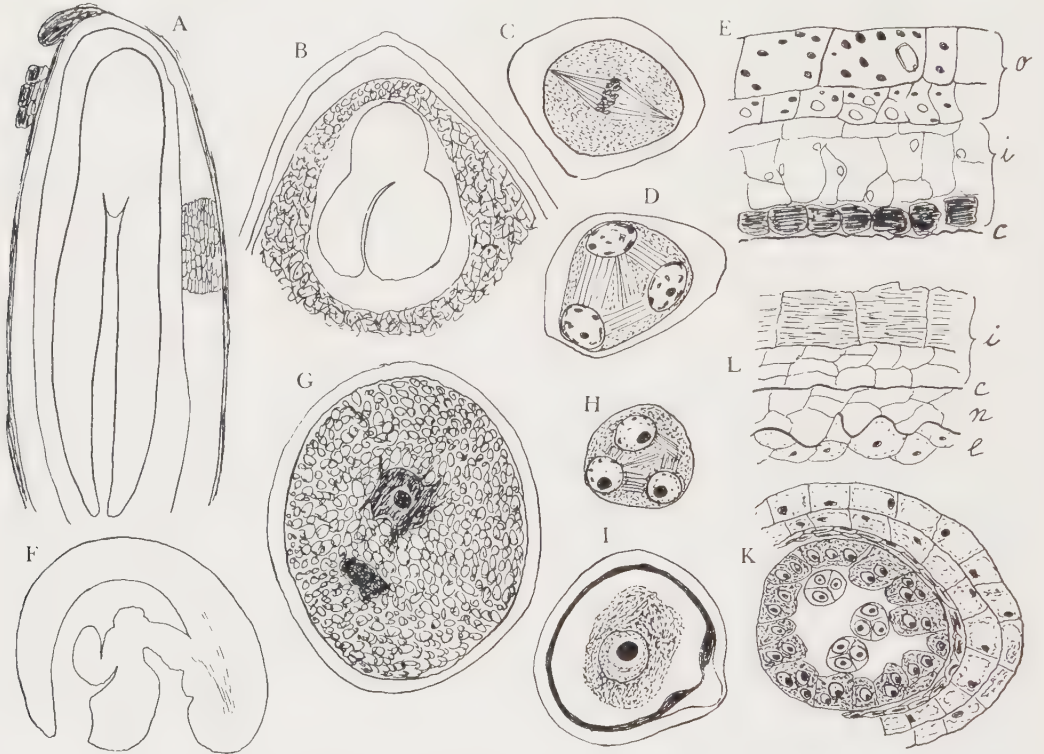


Fig 42. *A* *Alvaradoa amorphoides*. Seed with embryo; cellular, plasma-thin endosperm; seed coat. $\times 35$. *B* *Holacantha Emoryi*. Embryo and cellular endosperm. $\times 35$. *C-D* *Picrasma javanica*. *C* Heterotypic metaphase in pollen mother cell. $\times 1030$. *D* Homotypic telophase in ditto. $\times 1030$. *E-G* *Harrisonia Brownii*. *E* Seed coat. *o* outer, *i* inner integument, *c* cuticle. $\times 300$. *F* Mature embryo, the one cotyledon deformed. $\times 15$. *G* Mature pollen grain, 2-nucleate, with abundant reserve nutriment. $\times 900$. *H-K* *Irvingia malayana*. *H* Homotypic telophase in pollen mother cell. $\times 1030$. *I* 1-nucleate pollen grain. No reserve nutriment. $\times 1800$. *K* Transverse section through pollen chamber with pollen tetrads. $\times 400$. *L* *Suriana maritima*. Seed coat. *i* integument, *c* cuticle, *n* nucellus, *e* endosperm. $\times 300$.

geneous, vegetative. The anthers, however, do not abort immediately. In the male flowers the pollen development is normal. There arises also a rudimentary gynaeceum in these flowers which, however, does not form any ovary rooms, or these are only small empty cavities. Short styles occur. In *A. moluccana* there arises in the male flowers a rather massive gynaeceum with long styles, but only traces of ovary chambers could be detected. No signs of ovules occurred. In the male

flowers of *Picrasma javanica*, a fully normal gynaeceum arises with rooms and ovules which, however, at the time of the tetrad division in the anthers abort without showing any signs of differentiation. *Brucea* is polygamous. In the bisexual flowers normal pollen development occurs, not, however, in all anthers, as in some of these the contents of the pollen chambers degenerate. *Harrisonia*, *Irvingia*, *Samadera*, and *Quassia* are bisexual. *Picrodendron* is unisexual. I had only female flowers of this latter. Of the genus *Picrasma*, which is polygamous, I had only male flowers.

The wall in fertile anthers is quite normal with exothesium, endothesium, and tapetum, and between the last two one or two small-celled parietal strata. Fig. 42 K is a transverse section of a pollen chamber in *Irvingia malayana* with the above-mentioned layers evident. At the time of the tetrad division the tapetum is fully developed and then has often several nuclei in the cells. Later on the tapetum as well as the outer parietal layers becomes absorbed. No periplasmodium occurs. Later on the endothecium becomes fibrous.

Typical pollen mother cells in heterotypic prophase stages were observed in most of the species. Especially in *Picrasma javanica* I found synapsis, spirem, and diakinesis as well as all the main stages of the division, viz. heterotypical spindles, dyad nuclei, tetrad nuclei, and pollen tetrads. In the diakinesis the gemini could be counted to about 20. Fig. 42 C shows the heterotypical metaphase in this species. A rather thick cellulose wall existed. Fig. 42 D, H are homotypical telophases in *Picrasma* and *Irvingia malayana*. Simultaneous division takes place. Pollen tetrads were observed in all species with fertile anthers. The nuclei had tetrahedral, or quadratic position. The uninucleate pollen had still no reserve nutriment, the nucleus lay embedded in a portion of cytoplasm, otherwise the grain was empty. Fig. 42 I shows such a pollen grain in *Irvingia*. At one point of the wall the exine as well as the intine was thin and bulging. The mature pollen in this family is 2-nucleate, as stated by SCHÜRHOFF (l. c.), and, at least in *Ailanthus glandulosa* and *Harrisonia Brownii* whose ripe pollen I studied, as well as in *Meliaceae*, filled with reserve food (fig. 42 G). *Harrisonia* has very large pollen grains, even larger than in certain *Meliaceae* (see figs.). In *Ailanthus*, and in *Picrasma* they were about half the size of those in *Harrisonia*. The vegetative nucleus was often in the last mentioned species yellow-coloured, somewhat irregular, or lobate (fig. 42 G).

Burseraceae.

The family *Burseraceae* comprises only 16 genera, but the number of species amounts to approximately 600 (HARMS, in ENGLER and PRANTL 1931, p. 408), the family thus being on the whole equal in size to *Meliaceae*. It forms a rather natural unity most nearly related to *Rutaceae* and *Simarubaceae* from which *Burseraceae* differs by having resin and balsam canals in the bark. The family is an entirely tropical one, as it has no species outside this region. As ENGLER (l. c.) points out, there are in its distribution some ancient features.

No information about the development in this family is found in the literature. I had occasion to study 16 species representing 5 genera. Four species were of male nature, as they had abortive gynaecia. The species investigated are (ENGLER l. c.):

I. Protieae.	<i>Canarum balsamiferum</i> WILLD.
<i>Protium serratum</i> ENGL.	» <i>commune</i> L.
» <i>javanicum</i> BURM. (♂).	» <i>hirsutum</i> WILLD.
<i>Garuga floribunda</i> DECNE.	» <i>litorale</i> BL. (♂).
	» <i>longissimum</i> HOCHREUT. (♂).
II. Boswellieae.	» <i>nitidum</i> A. W. BENN.
<i>Commiphora</i> sp. I.	» <i>oleosum</i> ENGL.
» sp. II. ¹	» <i>patentinervium</i> MIQ. (♂).
III. Canarieae.	<i>Santiria nervosa</i> H. J. L.
<i>Canarium asperum</i> BENTH.	» <i>rubiginosa</i> BL.

The investigation comprised in the main only the earlier development of the ovule, as post-fecundated stages were but few in the material. This was received from the Botanic Garden at Buitenzorg, with the exception of *Canarium nitidum*

¹ These two species were sent to me from Madagascar undetermined, and as it was impossible for me to decide from the scanty material received what species they belong to I must for the present put them under the above indication. The genus *Commiphora* is a large one and still little analyzed. (see ENGLER 1931). The following 10 species are found in Madagascar: *Aprevalii*, *cuneifolia*, *fraxinifolia*, *grandifolia*, *greveana*, *madagascariensis*, *Marchandii*, *orbicularis*, *Pervilleana*, and *tetramera*.

which i have got from the Botanic Gardens at Singapore, and the two *Commiphora* species which were sent to me from Madagascar.

Gynaeceum. Genesis, number, and orientation of the ovules.

As regards the structure of flower and gynaeceum there are detailed statements given by ENGLER (1896, 1931). The flowers in *Burseraceae* are noted to be bisexual, but a common tendency to abortion of the one sex exists. Thus four of the species investigated are to be regarded as male ones, since gynaecea occurred in the flowers but produced no ovules. Of the others, *Garuga floribunda* and *Protium serratum* were fully normal, bisexual, producing normal ovules as well as pollen. A certain irregularity occurred, however, in these genera. Thus at times in *Garuga* one or other degenerating pollen sac was found, and in *Protium* the ovules were at the time of the formation of embryo sac and pollen rather plasma-thin. It may be presumed that they abort in later stages. In all other species studied, the flowers had in earlier stages both sexes fully normal. An archesporium is formed in the anthers which develops into a normal pollen sac with the usual wall layers and pollen mother cells. These latter pass through the heterotypic prophase stages but degenerate at the tetrad division, the anthers in later stages thus containing only black-coloured cell remnants. No fertile pollen is formed. These flowers are thus, in reality, unisexual, female.

The structure of the gynaeceum in this family is rather uniform without any important variations. It is throughout syncarpous and consists of 2—5 carpels. *Protium* and *Garuga*, and others, have most often 4—5 carpels, *Commiphora* 2, *Canarium* and *Santiria* 3, and a corresponding number of cells in the ovary. The figs. 43 B-D and G show transverse and longitudinal sections of the gynaeceum in *Canarium*, the greatest genus in this family comprising about 150 species. The gynaeceum is often flask-shaped with rather long and massive, often triangular ovary, as in fig. 43 G of the spec. *commune*. It narrows off quickly into a rather short style with three stigmata. The chambers are placed in the basal part. The transverse sections, fig. 43 B-C, show the three stigmata with their ventral furrows leading down into the ovary cells through rather long canals in the upper part of the ovary (C). There are two collateral ovules in each chamber (fig. 43 D).

The gynaeceum arises as a small rounded papilla in the centre of the flower. Even at an early stage the border of the papilla, in *Canarium*, begins growing at three different points, thus forming the three carpels. Inside these small cavities form the ovary chambers, as fig. 43 A shows. In this fig. the stamens grow up and the carpels bend in forming the ovary. On the bent-in margins the ovules arise. The margins grow together in the centre, the placentation thus being central and marginal. Fig. 43 H shows a young ovular papilla in *Canarium hirsutum*. The number of ovules in each partition is in *Burseraceae* constantly two. The space in early stages is rather roomy, as is seen in the afore mentioned figure, and is

similar in all species so far as I had occasion to study the matter. As development proceeds, the ovules fill up the whole chamber, as is evident in fig. 43 G, a. o. The two ovules in this family have all the time a collateral position, so that displacement in vertical direction as in *Meliaceae* does not take place (fig. 45 F).

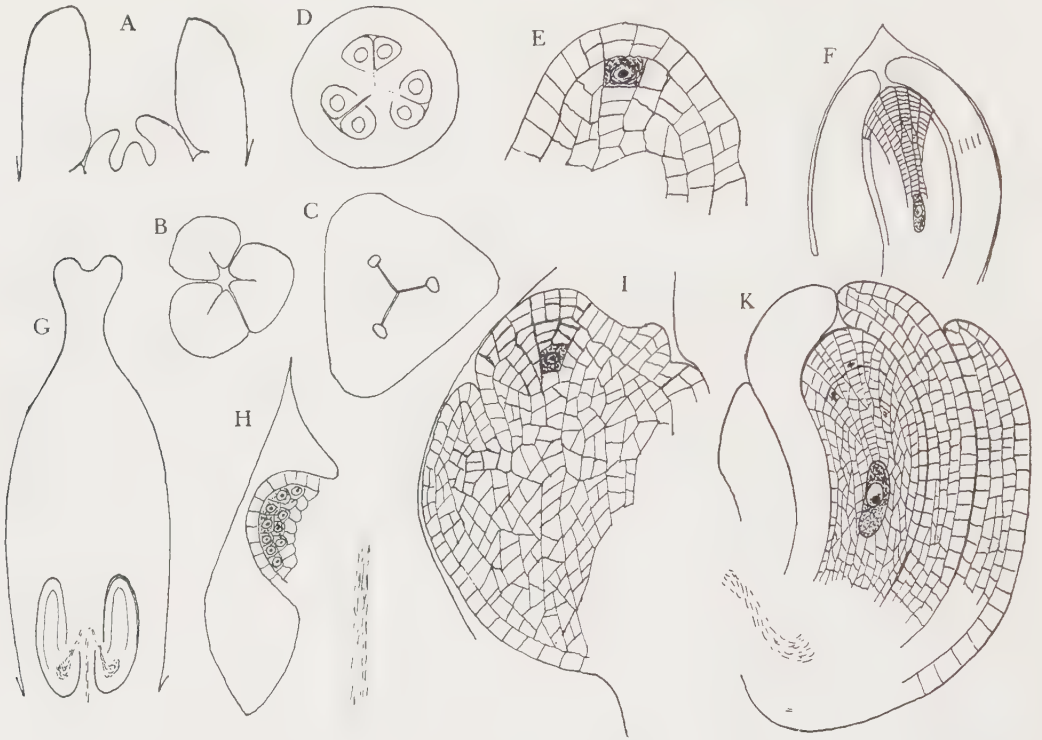


Fig. 43. A-C, *H Canarium hirsutum*. A Young gynaecium and stamens. The carpels closing and forming the ovary. $\times 50$. B-C Transverse sections of stigmata and upper part of the ovary. $\times 70$. H Longitudinal section of ovary chamber with young ovular papilla. Vascular strand in the placenta. $\times 185$. D *Canarium asperum*. Transverse section of ovary showing the collateral ovules. $\times 35$. E-F *Can. oleosum*. E Subepidermal archesporial cell. A periclinal division in an epidermis cell, indicating the origin of the integument. The nucellus cap arising. $\times 485$. F E. M. C. under about 18 tapetal cells plus 4 cap cells. The single integument is five-layered. $\times 185$. G, K *Can. commune*. G Longitudinal section through gynaecium. $\times 10$. K E. M. C. in synapsis under 13 tapetal cells and 4 cap cells. The micropyle is already closed. Nucellus campylotropous. $\times 185$. I *Can. balsamiferum*. Longitudinal section of young ovule with archesporial cell under 3 tapetal cells. Nucellus cap. The origin of the outer integument is indicated by periclinal division in three epidermis cells. $\times 300$.

The orientation of the ovules is in this family very uniform, epitropous, except in *Protium*, where they are directed downwards (fig. 45 C) and remain in this position at least until the embryo sac is built. Later stages were not included in the material. The position in *Protium* should probably be called hemiapotropous. The ovules remain in *Protium* straight, in other genera investigated they become more or less campylotropous or amphitropous, especially in later stages, as several

figs. show (e. g. 43 K, 44 A, B). Particularly in *Canarium* the nucellus and embryo sac become in later stages hook-formed in the chalaza, as is shown in fig. 46 F and 47 B.

Nucellus. Archesporium. Integument.

Burseraceae has crassinucellate and, as a rule, bitegmic ovules. As regards the development of the nucellus this family shows some interesting traits, mentioned below. The development of the ovules proceeds as follows in the different genera.

Canarium. A young ovular papilla in *C. hirsutum* is drawn in fig. 43 H. It arises on the middle part of the placenta and is still undifferentiated, but it is not long before archesporium and integument arise. Fig. 43 E shows the subepidermal archesporium cell in *C. oleosum*. The commencement of the integument, in this species a single one, is indicated by a periclinal wall in an epidermis cell on the outer side of the papilla. The early cap formation in the point is visible in this figure, too. A somewhat later stage is seen in fig. 43 I of *balsamiferum*. The rather thick ovule is still directed upwards, the inner integument grows out, somewhat stronger on the outer side, and the outer one, formed by periclinal division, is visible in the epidermis on the outer side. The rather lively cap formation in this genus is here evident, as still only three tapetal cells are formed. As a rule, the archesporium in *Canarium* seems to be one-celled. In early stages I have indeed seen one or two neighbouring cells with larger nucleus or nucleolus than other cells, but one cannot here speak of a many-celled archesporium.

At the time of the archesporial cell growing into embryo sac mother cell in *Canarium*, a remarkable growth of the nucellus point originates, in that the division of the tapetal cells takes place almost wholly in periclinal direction. Transverse division figures appear at this time very rarely in nucellus, whereas several longitudinal spindles are visible contemporaneously. At the same time the cap formation in the epidermis proceeds, ending, however, as far as I have been able to see, with a number of about 10 cell layers in later stages. The boundary between the cap and the original nucellus is not always easy to decide. The above development of the nucellus point results, in some later stages, in such figures as 43 F, K of *oleosum* and *commune*, and 44 A of *balsamiferum*. In all these cases the mother cell was still only in synapsis under: in *oleosum* about 18 parietal cells and 4 cap cells, in *commune* 13 plus 4, in *balsamiferum* under no less than about 20 parietal cells and 4 cap cells. The growth of the nucellus in breadth during the same time is rather insignificant. The nucellus is now long and of about uniform thickness, lengthened, pear-shaped, or sausage-shaped, or in *balsamiferum* almost tube-shaped. At the same time it grows campylotropous. As the figs. show the E. M. C., too, takes part more or less in the curvature. The division of the tapetal cells proceeds further, and the E. M. C. migrates down the nucellus into the chalaza. When the tetrad division begins I have counted in *commune*

no less than about fifty cell layers above the mother cell of which about ten were cap cells. The dyad in fig. 46 G is drawn from such an ovule. The dyads is curved as also the nucellus. Some further figs. elucidate the development of the

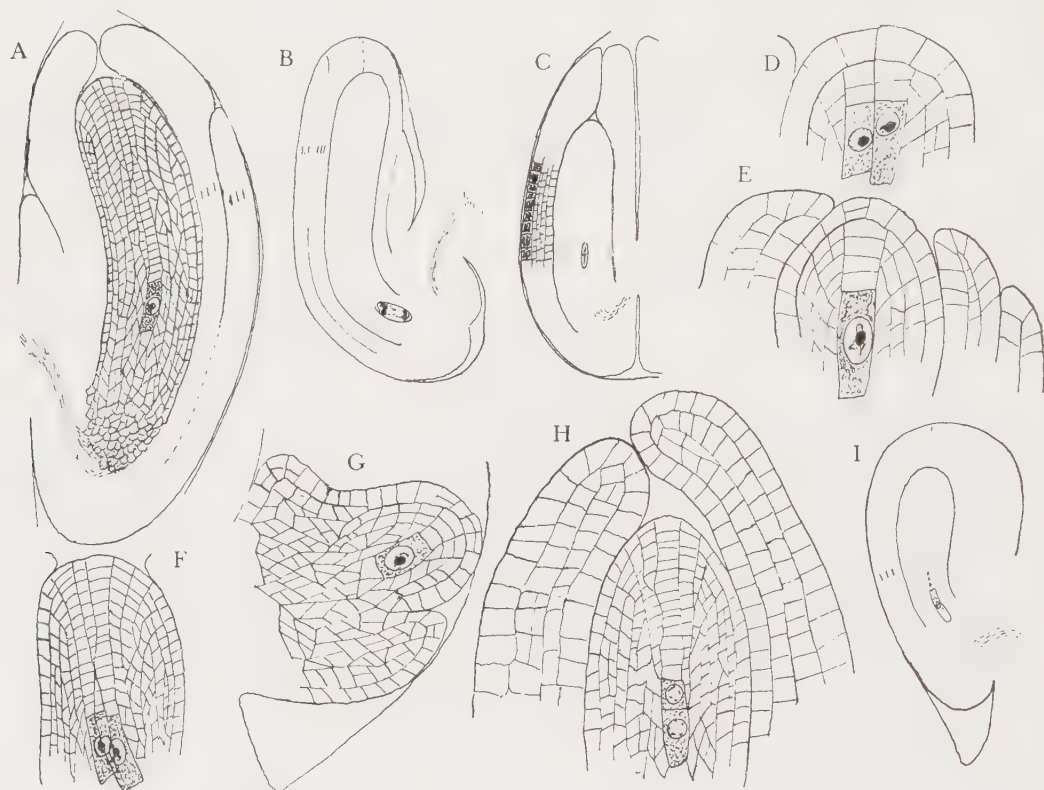


Fig. 44. *A* *Canarium balsamiferum*. *E. M. C.* in synopsis under about 24 cell strata. Nucellus long and narrow and campylotropous. The micropyle closed. The integuments 4-layered. A vascular strand entering the chalaza. $\times 185$. *B* *Can. commune*. The shape of the ovule when the *E. S.* is 4-nucleate. About 65 cell strata above the sac. $\times 70$. *C* *Can. asperum*. The ovule at the beginning of the tetrad division. The outer epidermis of the single, 5-layered integument is getting large-celled and resinous. Above the mother cell there are about 25 layers of cells. $\times 100$. *D-E* *Garuga floribunda*. *D* Two *E. M.* cells in synopsis. Two parietal cells. $\times 485$. *E* *E. M. C.* under four parietal cells. Integuments. $\times 400$. *F-I* *Santiria rubiginosa*. *F* Two *E. M.* cells under 13 cell layers. $\times 400$. *G* *E. M. C.*, 3 tapetal cells. The single integument growing out. The cap arising. $\times 300$. *H* Dyad under 14 cell layers. The 4-layered integument has closed into micropyle. $\times 300$. *I* The shape of the ovule when the tetrad division is completed. About 20 layers above the tetrad. $\times 100$.

nucellus in this genus. Fig. 44 B shows the position of a 4-nucleate embryo sac in *commune*. It is still short and situated down in the chalaza as far as possible. On account of the strong curvature of the nucellus at the chalazal end, the embryo sac is now almost at right angles to the upper part of the nucellus. Above this sac I counted about 65 cell strata. A similar 4-nucleate sac in the chalaza in

C. nitidum lay under no less than about 85 cell strata — no doubt a rather rare development of an ovule in plants! The thickness of the nucellus, on the other hand, was only about 15 layers. The nucellus in these species is now almost tube-like, as is seen in e. g. fig. 44 B. The development in these species has hitherto been located to the chalaza, i. e. the tetrad division, and the first nucleus divisions in the embryo sac. In the 4-nucleate stage the sac commences a growing in length upwards through the nucellus, absorbing and also compressing the tissue of tapetal cells. Fig. 47 B shows this development in *C. nitidum*. The sac in this ovule was still 4-nucleate but had attained considerable length, without, however, getting any increase in thickness. The same development takes place in *C. commune*. The number of cell strata between the top of the sac and the nucellus point in fig. 47 B was about 65, of which 10 were cap strata. In *commune* I saw in one case about 40 strata above such a long curved 4-nucleate embryo sac. Thus we see that in these species the 4-nucleate E. S. grows in length and absorbs about 20 or 25 cell layers before any further nucleus division takes place in the sac. In this position, however, the nuclei divide again, giving rise to 8-nucleate sacs. Thus I have in *commune* observed a ready built E. S. under about 45 cell strata. While waiting for fertilization the sac increases in length, absorbing more tissue. Thus the sac in fig. 46 F had its top under about 35 pressed and plasma-thin cell strata. One can also by comparison of figs. 44 B and 46 F get a certain idea of the increase in size of the embryo sac as well as of the entire ovule in this species during the development, as the figs. are drawn on the same scale.

The above development of the nucellus in *Canarium* is not quite the same in all species. As is mentioned above, *nitidum* is on the whole similar to *commune*, viz. as to the campylotropous shape of nucellus and embryo sac and the absorption of the parietal cells. *C. oleosum* has considerably smaller ovules than the two former species, as is evident from figs. 43 F and K drawn on the same scale. The embryo sac does not divide so far down in the chalaza as in those but only under about 25 strata of cells. The nucellus has indeed the same curved form, but the embryo sac does not enter into the curvature in this species, as is seen in fig. 47 E. Only in later stages, at the formation of the endosperm, does it become somewhat bent at the chalazal end (fig. 48 D). The absorption of the parietal cells in *oleosum* is somewhat less during the formation of the embryo sac. Thus the number of strata above the sac in fig. 47 E was about 20, in another case I saw 13 cell strata, etc. *C. asperum* is similar to *oleosum* as regards the size of the ovules (fig. 44 C). As in the other species, the nucellus is campylotropous in the chalaza but less so than in *commune* and *nitidum*. The embryo sac mother cell does not enter into the curvature, as it divides under only about 25 strata, shown in fig. 44 C. The number of tapetal cells seems not to increase later on in this species. As in other *Canarium* species, the embryo sac grows upwards absorbing the cells above, and in *asperum* the absorption is often so strong that there are only one or two cells left, or, at times, no cells at all between the sac and the point epidermis. In most cases, however, there were 10 to 15 cells left. While waiting for

fertilization the embryo sac seems to widen upwards as well as sideways, absorbing the nucellus. *C. balsamiferum* has a similar development of the nucellus to *commune* and *nitidum*. Its shape is curved, long and narrow, the size of the ovule is about the same as in those species (fig. 44 A). I had no later stages of *balsamiferum*, but it seems probable that the mother cell, as in *commune* and *nitidum*, migrates far down into the chalaza, and there passes through the earlier embryo sac development stages, as it had not come farther than to synapsis under 24 tapetal strata (fig. 44 A).

The development of the nucellus above described in *Canarium* is no doubt a rather rare one in plants. It is here the division of the tapetal cells that dominates. The number of cap strata seems limited to about ten or so. Some cases of similar development in other plants may be noted from the literature. First then I wish to mention the observations made above in the nearly related *Simarubaceae*. In *Brucea*, for instance, the tapetal strata were about 15 (plus five cap cells), and *Picrodendron* had about the same number. Still stronger nucellus had *Ailanthus malabarica* with an undivided E. M. C. under about 30 layers of which seven were cap cells (fig. 35 A). BERLESE (1892, pl. 12) has a good figure of *Vitis vinifera* with about 18 tapetal strata plus a nucellus cap of 10 layers strongly marked as a root cap. Also in *Malvaceae* rather strong tapetal cell complexes occur, as STENAR notes (1925, p. 29). The greatest number was found in *Althaea sulphurea* with 18 layers. Certain *Rosaceae* are characterized by a rather strong parietal cell formation, of which the inner cells develop into a many-celled archesporium. The cap, too, is here rather important, e. g. in *Alchemilla*. In *Meliaceae* *Aglaiia odorata* had a rather strong nucellus point (fig. 23 C).

A strong cap of epidermis cells is noted in many other plants. TÄCKHOLM (1923, p. 212) notes and draws a strong nucellus cap in certain *Caninae* of *Rosaceae*. FORENBACHER (1914, p. 90) mentions a cap in *Potentilla rupestris*, »die am Scheitel besonders ausgiebig erfolgen und dort eine mehrschichtige Kappe nach der Art einer Wurzelhaube schaffen». A somewhat stronger tapetal cell division was found by TÄCKHOLM (1915, p. 313) in *Godetia »Gloriosa»* and *Whitneyi* to an extent of about 30—40 layers in older ovules. No cap occurred. The embryo sac mother cells were also in these species placed far down in the chalaza. MAURITZON (1934 a) notes a rather considerable nucellus cap in *Phytolaccaceae*, in *Petiveria* 6—8 layers, in *Phytolacca*, *Rivinia*, and *Villamilla* 8—15 layers. The cap in these plants reaches farther down at the sides of the nucellus than in *Burseraceae*. The same author found nucellus cap also in *Cactaceae* (*Rhipsalis*, a. o.). Other families with epidermis cap are *Ranunculaceae* and *Gramineae*.

The integuments in *Canarium* are two in number except in *asperum* and *oleosum* which are unitegmic. The earliest stages observed are seen in the figs. 43 E and I, and have been mentioned above. The inner one arises at the same time as the archesporium. It grows rapidly during the above mentioned development of the nucellus point, so that long before the division of the mother cell it already closes into micropyle, as is shown in several figs. (43 F, and K, 44 A). As is evident

from figs. 43 K and 44 A the micropyle closes in *commune* and *balsamiferum* as early as in the synapsis stage in E. M. C., and the same seems to be the case also in *oleosum* (fig. 43 F). In *asperum*, which is unitegmie, the integument grows far up above the nucellus point, forming a rather long micropyle before the mother cells divide, as is seen in fig. 44 C. The mother cell is here just in heterotypic metaphase. Also *commune* and *nitidum* get a long micropyle but somewhat later, or at the formation of the embryo sac, figs. 44 B, 46 F and 47 B. In all the bitegmie species investigated the inner integument is 4-layered round the nucellus with the point swollen to about double thickness. I have seldom observed any deviations from this. The single integument in *oleosum* and *asperum* is 5-layered, somewhat swollen at the point in later stages (figs. 43 F, 44 C). The outer integument in bitegmie species of *Canarium* is somewhat retarded, as the figs. show. Probably it never reaches the top of the inner one. It is 4-layered in *commune* (figs. 43 K, 44 B, 46 F) and *balsamiferum* (fig. 44 A), with rare deviations. It does not swell at the point. At least in *commune* and *balsamiferum* I observed, in later stages, that the integuments, on the outer side grow together (figs. 44 A and 46 F); especially in the lower part, but also in the upper one the epidermis layers of the two integuments are often indistinct, the limit between them marked only by a somewhat thicker cellulose wall. If one had only such late stages at one's disposal, one would probably consider this species to be unitegmie, at least at first sight. A characteristic feature of this genus, probably caused by the peculiar growth of the nucellus, is that the outer integument occurs well developed also at the funicle side, as is shown in the above mentioned figures. It grows there somewhat slower in early stages (fig. 44 A-B), later, however, it reaches about the same height as on the outer side (fig. 46 F, 47 B). Its thickness is here about double that of the outer side.

As regards nucellus, archesporium, and integument in other genera, the following may be noted. Fig. 45 C shows the downward directed hemi-apotropous ovule in *Protium serratum*. As is evident from the scale, the ovules in this species are rather small in size. The nucellus is weak, with only one cell mantle round the archesporial cell. Later on indeed it grows somewhat thicker, but the tapetal cells seem never to be more than 3—4, and the epidermis cap is limited to one or two cell layers (fig. 47 A). The integuments are two in number, the inner one dominating, 3—4-layered; the outer is weaker, 2—3-layered, and developed round the nucellus. The integument closes at the tetrad division (fig. 47 A). The ovules at the formation of the E. S. were rather plasma-thin. I had no later stages.

Garuga floribunda has small ovules compared with e. g. *Canarium* (fig. 45 F). It is one of the few species studied that showed more than one archesporial cell. Fig. 44 D shows two well developed embryo sac mother cells in synapsis under two tapetal cells. I saw the same fact several times and, moreover, one or two cases where a tetrad, plus a parietal cell, developed into an accessory E. M. C., were found in one and the same nucellus. As a rule, only one cell develops further, as in fig. 44 E, where a rather large mother cell occurred under four cell

strata. Periclinal division begins in the point epidermis. The mother cell becomes moved forward far down into the chalaza before its division takes place, as fig. 45 F shows. In fig. 45 A the heterotypic division under eight tapetal cells and three cap layers is seen. Here the limit of the cap was distinctly visible. In ovules

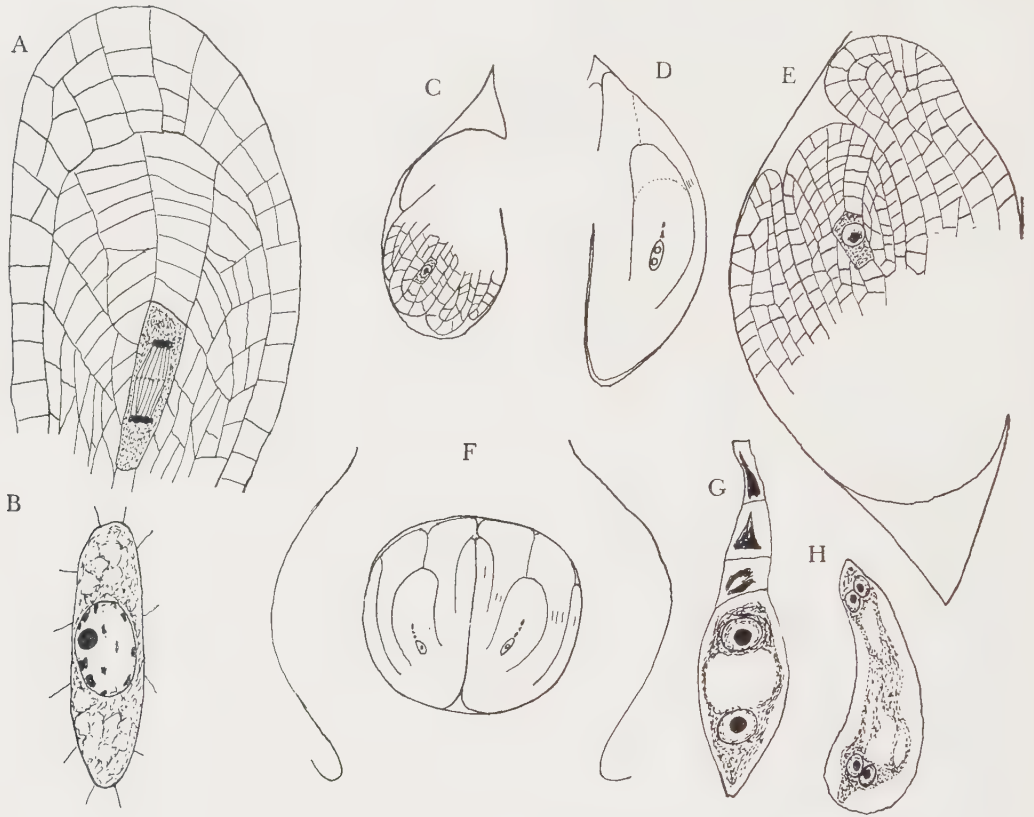


Fig. 45. *A, F Garuga floribunda*. *A* Heterotypic anaphase under 8 tapetal cells plus 3 cap cells. $\times 600$. *F* View of the collateral ovules in this family. Nucellus and integuments at the tetrad division. $\times 100$. *B Canarium oleosum*. *E. M. C.* in diakinesis. $\times 900$. *C. Protium serratum*. Hemiapotropous ovule. *E. M. C.*, two tapetal cells. Integuments. $\times 185$. *D-E, G Commiphora* sp. (II). *D* Nucellus and integument at the formation of the *E. S.* Nucellus cap indicated. $\times 80$. *E* *E. M. C.* in synapsis under six cell strata. Unitegm. $\times 300$. *G* 2-nucleate embryo sac. Tetrad remnants. $\times 900$. *H Canarium nitidum*. 4-nucleate embryo sac. $\times 300$.

of such a small size as those in *Garuga* the point tissue mentioned is rather remarkable. The ovules are also in this genus campylotropic, pear-shaped, thus with somewhat widened point, as in *Canarium* (fig. 45 F). The *E. S.* gets this form, too (fig. 46 I). There are two integuments, the outer one weak, 2-layered, and occurring also at the funicle side, with the same thickness; the inner integument is dominant, 3—4-layered, and becomes later on strongly swollen at the point (see fig.).

Fig. 44 G shows a young ovule in *Santiria rubiginosa*. The single integument grows out and the cap has begun in the point, the archesporial cell has already reached synapsis under three tapetal strata. The ovules are rather small (comp. fig. 44 I), the nucellus, however, is relatively well developed, and has rather strong point growth, as is seen in figs. 44 F, H. In the first mentioned fig. a tendency to the developing of two E. M. cells is evident. The strata above them were 13 or 14, of which only a few were cap cells. In another ovule I saw, besides a heterotypic spindle, an accessorial mother cell in synapsis (fig. 46 A). The tetrad division takes place under about 14 cell layers, as fig. 44 H shows. The cell strata increase in number later on, so that about 20 layers could be counted above the tetrad in fig. 44 I. The tetrad is moved forward into chalaza, in the same manner as in the former genera, and the nucellus assumes the same pear-shape as in those. *Santiria* is unitegmie. The integument closes at the tetrad division and is 4-layered (fig. 44 H); on the inner side it has about double that thickness (fig. 44 I).

The young ovule in *Commiphora* is fastened in the same manner as in other genera, viz, on the middle of the placenta (fig. 45 D-E). The ovules are relatively small (fig. 45 D). The earliest stage I saw was an archesporial cell under two tapetal cells. Fig. 45 E shows a somewhat later stage with an E. M. C. in synapsis under six layers, one or two of which are cap cells. The mother cell migrates down into the nucellus and divides under about 20 or 25 cell strata (fig. 45 D). The cap which here was rather distinct occupied about half the number and is thus in this genus rather large. The ovule is curved in the same manner as in other genera. *Commiphora* is unitegmie. The integument consists of about five cell strata, somewhat swollen in the upper part. Later on the embryo sac absorbs the nucellus, as in other genera, so that 10 or 15 cells remain in the point.

As a summary of nucellus, archesporium, and integuments in *Burseraceae*, the following may be noticed: As a rule this family has, owing to an unusual growth of the tapetal cells and also because of a rather abundant cap formation, strongly crassinucellate ovules. Because of this the embryo sac mother cell penetrates far down into the chalaza before its division takes place. The rather long and narrow nucellus and embryo sac become campylotropically curved, especially in *Canarium* in which the sac gets a hook-shaped curvature at the lower end. Later on the sac grows upwards absorbing the parietal cells. The integuments are two in number, except in *Canarium oleosum* and *asperum*, *Santiria rubiginosa*, and *Commiphora*, which are unitegmie.

Tetrad division. Formation of the embryo sac.

The tetrad division. During migration down into the nucellus the mother cell passes through the heterotypic prophase stages which have been observed in most of the species. Because of this feature one may presume that the division of the

mother cell is combined with chromosome reduction. The synapsis stage was often observed, as has been stated above (see figs.). A mother cell in diakinesis of *Canarium oleosum* is drawn in fig. 45 B, the same cell as in fig. 43 F. The number of the chromosomes could not be certainly fixed, it seems not, however, to be very

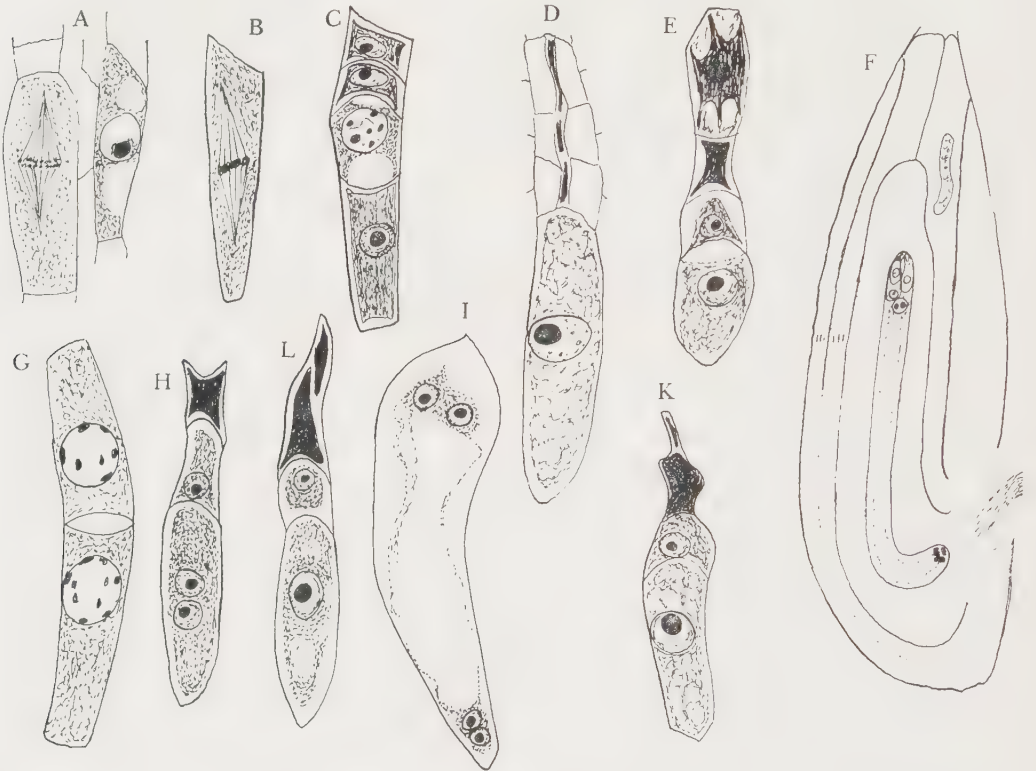


Fig. 46. A, H, L *Santiria rubiginosa*. A Heterotypic division. Accessorial E. M. C. in synapsis. $\times 830$. H 2-nucleate E. S(?). $\times 1030$. L Tetrad with primary 1-nucleate E. S. $\times 1030$. B-C, K *Canarium asperum*. B Heterotypic metaphase. $\times 830$. C Tetrad with the nethermost cell but one in growth. $\times 1030$. K Normal megaspore germination. $\times 900$. D, F-G *Can. commune*. D Primary E. S. Tetrad remnants. $\times 900$. F The shape of the ovule at the ripening of the E. S. The limit between the integuments on the outer side is indistinct. The outer integument strongly developed also on the inner side of the ovule. Secretion vesicle in the integument. $\times 70$. G Dyad. $\times 900$. E, I *Garuga floribunda*. E Tetrad. The uppermost cell has been in growth. $\times 900$. I 4-nucleate E. S., campylotropously curved. $\times 400$.

high. Several heterotypic spindles were observed, e. g. in *Canarium asperum*, fig. 46 B, in the ovule drawn in fig. 44 C. The tapetal cell development was mentioned above. In agreement with the shape of the nucellus in this species the cell and the spindle are long and narrow. Judging from the position of the nucleus plate the lower dyad cell here should probably have become the larger one. Fig. 46 A shows a heterotypic metaphase in *Santiria rubiginosa*. This as well as the cell is here broader and shorter. In this case, too, the lower dyad cell should have become

larger than the upper one. An accessory E. M. C. in synapsis occurred. Heterotypic division was observed also in *Garuga floribunda*, fig. 45 A, viz. an anaphase with incipient wall formation in the equatorial plane. The division should have resulted in a larger chalazal cell, to judge from the situation of the cell plate. The top structure in this ovule is mentioned above.

The heterotypic nucleus division is combined with cell division, so that dyad cells arise. Dyads were observed in several species, e. g. in *Santiria rubiginosa*, fig. 44 H. The lower cell dominated. Fig. 46 G shows a dyad in *Canarium commune*, also with dominating nether cell. This dyad had arisen farthest down in the curved chalaza in this species (fig. 44 B), which also its shape indicates. The long and narrow form of the cells, too, corresponds with the general shape of the nucellus in this species. The wall between the cells was lens-shaped. The nuclei were rather large, and each contained about twenty chromatin bodies. Already from the position of the nuclei one may presume that homotypic division would result in a tetrad in which the nethermost cell was the largest one.

The dyad cells divide and give rise to tetrads of four cells, and this normal type of tetrad division I have established in all the five genera studied. Only row tetrads were observed. Figs. 46 C, D, K show some tetrads in *Canarium*; figs. 46 E, H, and 48 A in *Garuga* and *Santiria*, and figs. 45 G, 47 A in *Commiphora* and *Protium*. In *Garuga* one case of retarded division in the upper dyad cell was observed, fig. 48 F. This figure cannot be suitably explained in any other way. An evident metaphase was visible with spindle threads, the cell, however, tended to degeneration. Below this there were a vital cell and a third one, undergoing degeneration, too. It seems probable that the uppermost cell is one of the dyads. In *Santiria rubiginosa* I saw a peculiar tetrad which can be explained in various ways, fig. 46 H. The nethermost cell had two nuclei close to each other without any sign of wall between them; above this there were one vital, and, so far as I was able to see, only one degenerating cell. The lowest cell may possibly be a 2-nucleate embryo sac, although the position of the nuclei contradicts this presumption; or the whole is a tetrad, the nethermost cell thus one of the dyads with retarded and deviating division.

As to the further development of the megaspores, the following may be noticed. In *Canarium* some variations were observed, although they do not shake the presumption that the nethermost tetrad cell, as a rule, normally develops into an embryo sac and the upper ones become absorbed. Fig. 46 D shows a normal case in *Canarium commune*, fig. 46 K another in *asperum*. Fig. 46 C, on the other hand, shows a deviating case of megaspore development in the latter species. It is evident that the nethermost tetrad cell here originally had the upper hand, but later on has begun to degenerate. The plasma was too dark for a vital cell. Above this cell there was a vital one with vacuolized cytoplasm and a large nucleus with chromatin grains, the cell thus probably being in a state of growth. The two upper cells were degenerating although with still visible nuclei. Fig. 47 A shows normal megaspore germination in *Protium serratum*, and no other

arrangement was observed in this species. This, however, was found several times in *Garuga floribunda*, besides many normal cases. Thus *Garuga* showed several tetrads with tendencies to further development of the micropylar megaspore, e. g. fig. 46 E. In this tetrad the uppermost cell was degenerating, the black-coloured

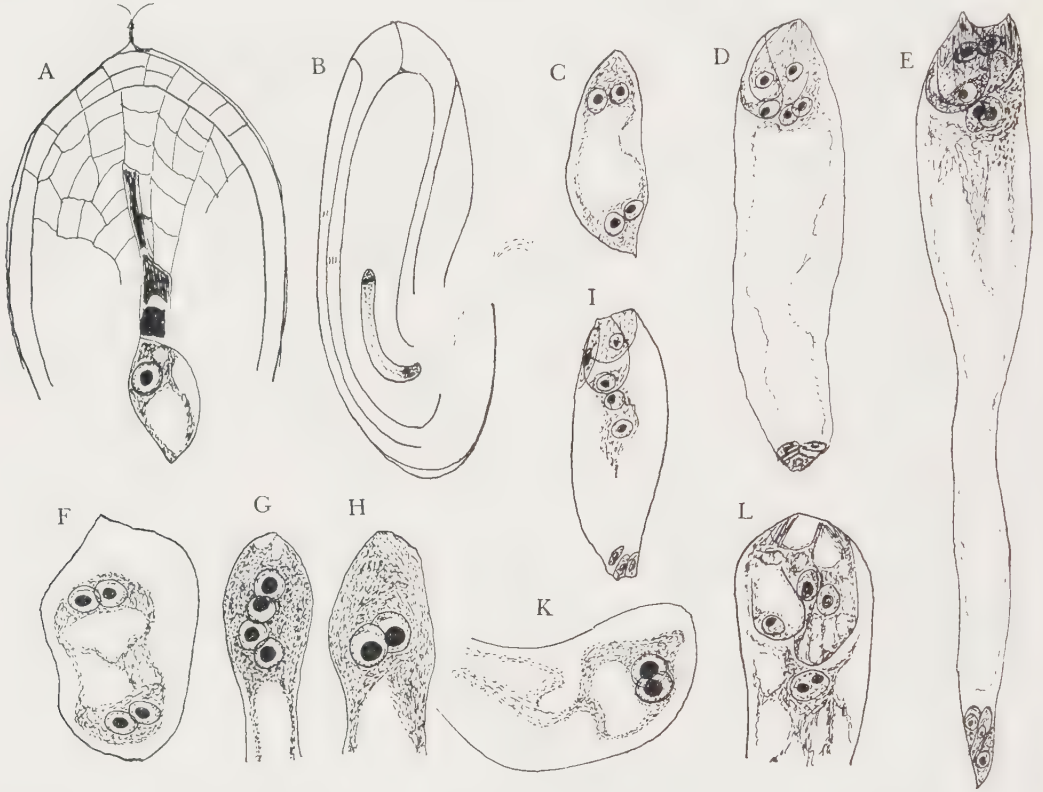


Fig. 47. A, F *Protium serratum*. A 1-nucleate E. S. with tetrad remnants. The micropyle is closed. $\times 900$. F 4-nucleate E. S. $\times 900$. B, G-H, K *Canarium nitidum*. B The shape of the ovule at the time of the 4-nucleate E. S. About 65 cell strata above the sac. $\times 70$. G The upper end of an 8-nucleate E. S. $\times 400$. H, K The two extremities of the sac drawn in fig. B. $\times 485$. C, L *Can. commune*. C 4-nucleate E. S. before growing (the same as in fig. 44 B), see the text. $\times 485$. L The E. S. mature for fertilization. Primary endosperm nucleus. $\times 300$. D *Can. asperum*. Mature E. S. $\times 300$. E *Can. oleosum*. Mature E. S. Comparatively strong point structure in the synergids. The three antipodals vital. $\times 300$. I *Commiphora* spec. (II). E. S. $\times 300$.

plasma-remnant, however, showed evident traces of vacuolization, and besides, the size of the cell indicated that it had been in growth. Fig. 48 A is an example of quite normal development in this genus. Fig. 48 F was mentioned above. Here it is evident that the nethermost megaspore but one would have become an embryo sac. *Santiria* showed normal megaspore germination, fig. 46 L. As to fig. 46 H, see above. Also *Commiphora* had quite normal megaspore development (fig. 45 G).

Formation of the embryo sac. As stated above, the chalazal megaspore in this family, as a rule, develops into embryo sac, according to the normal type. Several figures show such growing primary embryo sacs, e. g. figs. 46 D-E, K-L. In all cases the nucleus lay in the middle or upper part of the sac. In *Protium* the sac was rather vacuolized (fig. 47 A). As is seen e. g. in figs. 46 D, K, L, the sac increases considerably in size before the division of the nucleus takes place. After this division, polarity takes place and a vacuole occupies the middle part of the sac, as in fig. 45 G. After further growth of the sac the two nuclei divide again with retained vacuolization. Figs. 45 H, 46 I, 47 C, F, H-K show 4-nucleate embryo sacs in different species. About these it can be said that the 4-nucleate sac in *Canarium commune* and *nitidum* arises far down in the curved chalaza, as fig. 44 B shows. Higher magnification of this sac is seen in fig. 47 C. A similar sac in *nitidum* is visible in fig. 45 H. At that time the sac is short but is nevertheless, on account of the strong curvature of the nucellus, rather strongly bent, as the figs. show. These sacs are otherwise quite normal. Later on 4-nucleate sacs are found in these species of the shape shown in fig. 47 B, being lengthened into long tubes, strongly curved, with two nuclei embedded in plasma in each extremity and connected by a thin plasma veil. A stronger magnification of the nuclei is seen in fig. 47 H-K. Similar sacs were seen also in *commune*, in several cases. As was mentioned above, with regard to the development of the nucellus in these species, it is evident that the 4-nucleate embryo sacs in these lengthen in a rather remarkable manner before any further division of the nuclei takes place. During this growing the lower tapetal cells become absorbed, the upper ones, on the other hand, become compressed and get a thin plasma. The number of parietal cells was mentioned above.

Of the other *Canarium* species analogous stages were not included in the material, as was mentioned in the preceding chapter, but the division of the E. M. C. and the development of the embryo sac in *oleosum* and *asperum* do not take place so far down in the chalaza as in the above species (fig. 44 C). The sacs thus lack the curvature occurring in *commune* and *nitidum*. The upward growth of the sac in *oleosum* and *asperum* with absorption of tissue was touched upon before. Thus the heterotypic spindle in fig. 44 C of *asperum* lay under about 25 cell strata; above the ready built E. S. in fig. 47 D there were, however, only six layers. In other cases there were found ten, or fifteen cells, etc., and in some ovules the sac had absorbed all parietal cells up to the epidermis. Concerning *oleosum*, and *balsamiferum*, see the preceding chapter.

The early nucleus divisions in the E. S. in other genera have not shown any remarkable features, as far as I was able to examine them. Fig. 47 F shows a 4-nucleate sac in *Protium serratum*; fig. 45 G a sac of *Commiphora*. From fig. 46 I it is evident that the 4-nucleate E. S. in *Garuga floribunda* enters into the campylotropous curvature of the nucellus. Also in this genus an absorption of the nucellus takes place during the growing of the sac, so that of the approximately

11 tapetal strata occurring at the tetrad division (fig. 45 A) there were only six left above the 4-nucleate E. S.

The position of the nuclei with regard to each other in the 4-nucleate sacs mentioned above was that in most cases they lay abreast (see figs.), but if the sac was narrow, as in *Garuga* (fig. 46 I), the nuclei lay in a row.

When the 4-nucleate embryo sac in *Canarium* has received its definitive size a final nucleus division takes place, observed in *nitidum*, fig. 47 G. Further absorption of parietal cells had then occurred, the number of them above the 8-nucleate sac thus being about 45. A rather remarkable fact concerning these long embryo sacs is that the nucleus division seems to occur quite simultaneously at both ends, indicating that, probably, some stimulating substance occurs in the embryo sac. Also in other genera the nucleus division, so far as I have observed the matter, takes place simultaneously.

Completely built embryo sacs were observed in most of the species. They seemed normal, with egg apparatus, antipodal apparatus, and polar nuclei, as usual. In *Protium serratum* I once saw two embryo sacs in one and the same nucellus, indicating that in this species, though probably seldom, there occurs a many-celled archesporium. Some figures illustrate the ripe embryo sacs. Fig. 47 E shows a sac in *Canarium oleosum*. It was very long (about 350 microns, or $\frac{1}{3}$ mm.) and, especially at the lower end, narrow but straight, indicating that it had not formed part of the curvature of the nucellus. The egg apparatus was normal, the synergid nuclei were placed in the upper part of the cells, the egg nucleus, however, in the lower part. Point structure occurred, the polar nuclei had contact close below the egg apparatus. The antipodals are three in number, small and compressed in the tip of the sac. They seem, however, vital. Fig. 47 D is a sac of *C. asperum*, drawn on the same scale as the former which indicates the difference in size between them. It had a different shape from that in *oleosum*. The egg apparatus and polar nuclei had the same feature as in this species, the antipodals were three in number, rather insignificant but not quite absorbed. Fig. 47 L shows the upper end of a sac in *C. commune*, on the same scale. The synergids were here not quite normal. The points were vacuolized, and had thread structure, the nuclei lay in the middle part of the cells; the egg cell was normal, the polar nuclei had fused into a primary endosperm nucleus. The antipodals remained but were small. A general view of a similar sac in the same species is seen in fig. 46 F. The long, tube-like shape of the sac with the hook-formed chalazal end may be observed. Another remarkable circumstance in these sacs is the migration of the chalazal polar nucleus the long distance up to the upper end of the sac through the thin plasma veil which connects the two nucleus groups.

A rather mature E. S. in *Commiphora* is seen in fig. 47 I. It was in the main normal in structure, at least the egg cell; the polar nuclei meet in the vicinity of the egg apparatus; the antipodals are three in number, small. Fig. 48 K is a transverse section of the upper extremity of an ovule in *Protium serratum* with

the inner integument, nucellus and egg apparatus plus one of the polar nuclei. Fig 48 B shows a ripe, probably fertilized embryo sac in *Garuga floribunda*. The campylotropous, sausage-like form may be observed. The egg apparatus seemed

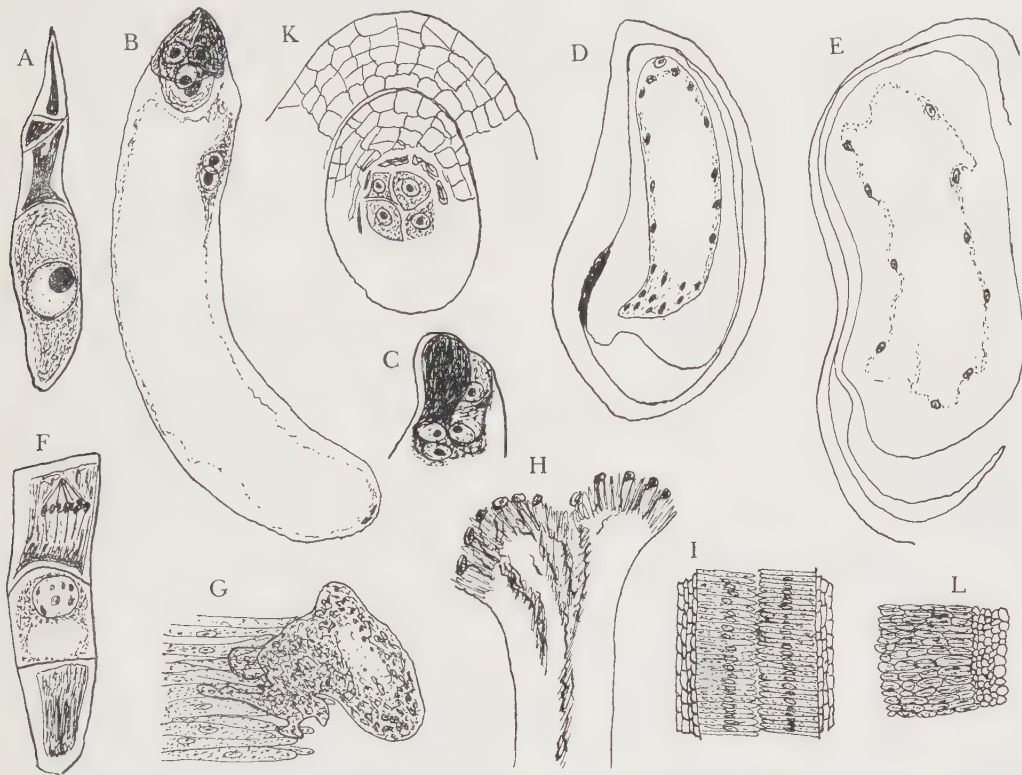


Fig. 48. A-C, F-I *Garuga floribunda*. A Primary embryo sac with tetrad remnants. $\times 1030$. B Probably fertilized E. S. $\times 400$. C Fertilized E. S. $\times 400$. F The upper dyad cell in retarded division. The middle cell constituting the E. S. $\times 1030$. G A swollen pollen tube on the stigma. The hairs are long cells. $\times 300$. H Germinating pollen on the stigma, and pollen tubes in the style. $\times 35$. I Palisade epidermis in the stylar canal. $\times 300$. D *Canarium oleosum*. Young seed with nuclear endosperm. The egg cell abortive. $\times 35$. E *Santiria rubiginosa*. Young seed with nuclear endosperm. $\times 35$. L *Canarium commune*. The hairs on the stigma are cell threads. $\times 100$. K *Protium serratum*. Transverse section of the upper end of an ovule, showing inner integument, nucellus, egg apparatus and polar nucleus. $\times 400$.

on the whole normal, the polar nuclei had contact on the one side; the antipodals were already absorbed. No embryo sacs occurred in the material of *Santiria*.

The development after fecundation.

About the further development of the embryo sac in this family I have but little to say, as the material was too scarce for this purpose. I have, however, seen pollination at least in one genus and have also been able to establish the type of the endosperm in some cases.

The conductive tissue begins on the stigmata with a hairy or papillous epidermis, see e. g. fig. 48 L of *Canarium commune*, or *Garuga*, figs. 48 G-H. In the first mentioned genus the hairs consist of cell threads, in *Garuga*, on the other hand, of long cells, as the figs. show. This ectotrophic tissue continues in this genus down into the stylar canal with an epidermis of long, narrow, or palisade-like, plasmons cells, as in fig. 48 L. I have observed practically the same circumstance in *Canarium asperum*.

Pollination was observed in *Garuga*. Numerous germinating pollen grains in different stages of growth were found in the hairs on the stigma (fig. 49 F), and the stylar canal showed a confusion of pollen tubes, fig. 48 H. In fig. 48 G I have drawn a peculiar, swollen and lobate tube on the stigma, containing an abundance of albumen grains. The pollen tubes are rather feeble and were not distinctly visible in the micropyle or nucellus, but the fertilization of the sacs drawn in figs. 48 B and C seems quite certain. Many sacs with the same appearance were observed in this species. In fig. 48 B one of the synergids was strongly coloured although not quite disorganized. The dark-coloured nucleus was still visible. Close to the egg nucleus I saw a black body which was probably one of the sperm nuclei. The other one could not surely be distinguished. Fig. 48 C shows an evidently disorganized synergid, wherefore this sac was probably fertilized, although I did not see the sperm nuclei. The polar nuclei lay close below the egg apparatus. Porogamy no doubt prevails.

No embryos were found. Nuclear endosperm was, however, observed in *Canarium oleosum* and *Santiria rubiginosa*. Fig. 48 D shows a section of a young seed in the former species, containing a large embryo sac with a thin plasma stratum at the wall in which some scattered endosperm nuclei occurred somewhat accumulated in the chalazal end. At the upper end of the sac there was found the undivided, probably abortive egg cell. Assuming normal development, a rather advanced embryo should have occurred in this embryo sac. Nor did any embryo occur in the seed of *Santiria rubiginosa* drawn in fig. 48 E, but only a sparse nuclear endosperm. As to embryo and seed, see also ENGLER (1931).

The seed coat. NETOLITZKY (1926) notices the lack of information about the seed testa in this family. In the young seeds I have seen of *Santiria rubiginosa* and *Canarium oleosum*, the testa is formed of the single integument occurring in these species. The outer epidermis develops into a large-celled, resinous stratum (fig. 44 C). In the bitegmic species both the integuments share in the formation of the testa, with the same structure of the outer epidermis as was mentioned. All the cell layers become later on more or less resinous.

Pollen development.

As was mentioned before, the earlier stages of the development of the anthers are quite normal in all flowers. At the time of the tetrad division in the pollen mother cells, however, the pollen sacs degenerate in bisexual flowers, or at times

earlier, as in *Santiria rubiginosa*. Fig. 49 A is a transverse section of a pollen sac in *Canarium hirsutum* (the same flower as in fig. 43 H). A fertile gynaeceum occurred in the same flower. The pollen sac is normal; the pollen mother cells have reached the diakinesis stage. The anther wall had the normal layers, viz. tapetum, with one or more nuclei in the cells, further a couple of small-celled strata, and, finally, endothecium and exothecium. The development of the anther ceases about this time. Later on the sacs contain only black-tinged remnants of cells, become compressed, the wall does not develop further, the whole anther becomes plasma-thin and, finally, degenerates. This progress does not take place in *Garuga floribunda* and *Protium serratum*, in which the development pro-

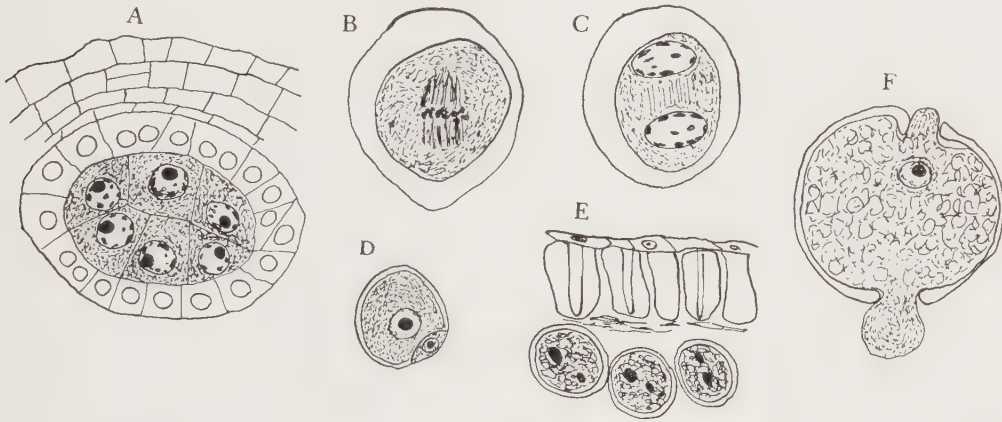


Fig. 49. A *Canarium hirsutum*. Transverse section of pollen chamber showing a normal wall and pollen mother cells in diakinesis. $\times 485$. B-C *Canarium littorale*. Heterotypic division in pollen mother cell, and dyad nuclei. $\times 900$. D *Protium serratum*. Lens-shaped generative cell detached. $\times 900$. E-F *Garuga floribunda*. E Fibrous layer; 2-nucleate pollen; tapetum absorbed. $\times 300$. F Germinating pollen grain. $\times 900$.

ceeds normally to fully fertile pollen. Here the anther wall, too, gets the usual appearance with fibrous stratum.

In species with male character, as *Protium javanicum*, *Canarium littorale*, *longissimum*, and *patentinervium* the development in the anthers is fully normal. Heterotypic division was observed in *Canarium littorale*, fig. 49 B. In a diakinesis of this plant I counted about 18 chromosomes. In the same species also dyad nuclei were seen (fig. 49 C). Simultaneous wall formation occurs. Pollen tetrads were found in *Commiphora* (II), also indicating the same type of pollen division. The 1-nucleate pollen contains no reserve food; later on, however, the grains become filled with nutriment, thus getting the same appearance as in *Meliaceae* (fig. 30 B), or *Simarubaceae* (fig. 42 G). A lens-shaped generative cell was observed in *Protium serratum* (fig. 49 D), and in *Garuga*. In pollen sacs of *Protium* and *Garuga* with fully developed fibrous stratum I have seen 2-nucleate pollen (fig. 49 E), so that, in *Burseraceae*, the generative nucleus probably does not divide until pollination

has taken place. Thus, in this respect as well as in the occurrence of the reserve food, this family agrees with those mentioned above.

The size of the pollen in *Garuga* is rather considerable (fig. 49 F), although not as large as in certain *Meliaceae*. In *Protium serratum* the pollen is about half the size of that in *Garuga*.

The gynaecea occurring in the male flowers are in most cases small and insignificant, in *Protium javanicum*, however, rather large, having also style and stigma. In no cases have I seen any ovules in them, and often no chambers, the gynaeceum then consisting only of vegetative tissue.

Bibliography.

1916. AFZELIUS, K., Zur Embryosackentwicklung der Orchideen. Sv. Bot. Tidskr., 10.
1931. ANDERSSON, A., Studien über die Embryologie der Familien *Celastraceæ*, *Oleaceæ* und *Apocynaceæ*. Lunds Univ. Årsskr. N. F., 2, 27.
1920. ASPLUND, E. Studien über die Entwicklungsgeschichte der Blüten einiger Valerianaceen. Kgl. Sv. Vet. Ak. Handl., 61.
1927. BAILEY, L. H., The Standard Cyclopedia of Horticulture. New York.
1859. BAILLON, H., Monographie des Buxacées et des Stylocérées. Paris.
1883. BENTHAM, G. et HOOKER, J. D., Genera plantarum, III. Londini.
1892. BERLESE, A. N., Studi sulla forma, struttura e sviluppo del seme nelle Ampelideæ, Malpighia, 6.
1901. BILLINGS, F. H., Beiträge zur Kenntnis der Samenentwicklung. Flora, 88.
1913. BOAS, F., Beiträge zur Anatomie und Systematik der Simarubaceen. Beitr. Bot. Centralbl., XXIX.
1859. BRAUN, A., Über Polyembryonie und Keimung von *Cælebogyne ilicifolia*. Abh. Berl. Ak. Wiss.
1916. BREMER, G., Reliquiæ Treubianæ II. Ann. Jard. Bot. Buitenzorg, 2.
1922. BRENNER, W., Zur Kenntnis der Blütenentwicklung einiger Juncaceen. Acta soc. sc. Fenn., 50.
1921. BÖÖS, G., Neue embryologische Studien über *Alchemilla arvensis* Scop. Bot. Notis.
1926. CARANO, E., Ulteriori osservazioni su *Euphorbia dulcis* L. in rapporto col suo comportamento apomittico. Ann. di bot., 17.
1893. CELAKOWSKY, L., Über den Fruchtknoten von *Pachysandra procumbens* Michx. Österr. bot. Zeitschr., 43.
1870. CHATIN, A., De l'anthere. Paris.
1874. —, Organogénie comparée de l'androcée, dans ses rapports avec les affinités naturelles. Compt. rend. acad. sci., 78. Paris.
1913. COHN, F. M., Beiträge zur Kenntnis der Chenopodiaceen. Flora, 106.
1903. COULTER, J. M. and CHAMBERLAIN, CH. J., Morphology of Angiosperms. New York.
1915. DAHLGREN, K. V. O., Über die Überwinterungsstadien der Pollensäcke und der Samenanlagen bei einiger Angiospermen. Sv. Bot. Tidskr., 9.
1916. —, Cytologische und embryologische Studien über die Reihen *Primulales* und *Plumbaginales*. Kgl. Sv. Vet. Ak. Handl., 56.
1923. —, Notes on the ab initio cellular endosperm. Bot. Notis.
- 1927—28. —, Die Morphologie des Nucellus mit besond. Berücksichtigung der deckzelllosen Typen. Jahrb. wiss. Bot., 67.
1928. —, Hakenförmige Leistenbildungen bei Synergiden. Ber. d. d. bot. Ges., 46.
- 1875—78. EICHLER, A. W., Blüthendiagramme. I, II. Leipzig.
- 1873—77. ENGLER, A., Studien über die Verwandtschaftsverhältnisse der *Rutaceæ*, *Simarubaceæ* und *Burseraceæ*. Abh. naturf. Ges. Halle, 13.
- 1896, 1931. —, *Simarubaceæ*, in ENGLER—PRANTL. Die natürl. Pflanzenfam. 1896. 2. Aufl. 1931.

- 1896, 1931. ENGLER, A., *Burseraceae*, in ditto.
1901. ERNST, A., Beiträge zur Kenntnis der Entwicklung des Embryosackes und des Embryo (Polyembryonie) von *Tulipa Gesneriana* L. Flora, 88.
1909. —, Apogamie bei *Burmannia coelestis* Don. Ber. d. d. bot. Ges., 27.
1913. —, Zur Kenntnis von Parthenogenesis und Apogamie bei Angiospermen. Verh. schweiz. naturf. Ges.
1918. —, Bastardierung als Ursache der Apogamie im Pflanzenreich. Jena.
1909. —, und SCHMID, E., Embryosackentwicklung und Befruchtung bei *Rafflesia Patma* Bl. Ber. d. d. bot. Ges., 27.
1916. FARR, C. H., Cytokinesis of pollen-mother cells of certain dicotyledons. Mem. New York Bot. Gard., 6.
1917. FAWCETT, W. and RENDLE, A. B., Notes on Jamaica Plants. Journal of Bot. Lond.
1914. FORENBACHER, A., Die Fortpflanzungsverhältnisse bei der Gattung *Potentilla*. Bull. trav. nat., Zagreb.
1912. FRISENDAHL, A., Cytologische und entwicklungsgeschichtliche Studien über *Myricaria germanica* Desf. Kgl. Sv. Vet. Ak. Handl., 48.
1908. GEERTS, J. M., Beiträge zur Kenntnis der cytologischen Entwicklung von *Oenothera Lamarckiana*. Ber. d. d. bot. Ges., 26 a.
1907. GIBBS, L. C., Notes on the development and structure of the seed in the *Alsinoideae*. Ann. of Bot., 21.
1923. GOEBEL, K., Organographie der Pflanzen. III. Jena.
1928. —, Ditto, I.
1921. HABERLANDT, G., Über experimentelle Erzeugung von Adventivembryonen bei *Oenothera Lamarckiana*. Sitz. ber. Preuss. Ak. Wiss.
1922. —, Die Vorstufen und Ursachen der Adventivembryonie. Ibidem.
1923. —, Über die Ursache des Ausbleibens der Reduktionsteilung in den Samenanlagen einiger parthenogenetischer Angiospermen. Ibidem.
1925. —, Zur Embryologie und Cytologie von *Allium odorum* L. Ber. d. d. bot. Ges., 43.
1927. —, Zur Cytologie und Physiologie des weiblichen Gametophyten von *Oenothera*. Sitz. ber. Preuss. Ak. Wiss.
1896. HARMS, H., *Meliaceae*, in ENGLER-PRANTL: Natürl. Pflanzenfam., III.
1885. HEGELMAIER, F., Untersuchungen über die Morphologie des Dikotyledonen-Endosperms. Nova Acta Leop. Carol. Akad. Nat., 49.
1897. —, Zur Kenntnis der Polyembryonie von *Allium odorum* L. Bot. Zeit., 55.
1901. —, Über einen neuen Fall von habitueller Polyembryonie. Ber. d. d. bot. Ges., 19.
1903. —, Zur Kenntnis der Polyembryonie von *Euphorbia dulcis* Jacq. (*purpurata* Thuill.). Ibidem, 21.
1922. HOFFGEN, FR., Serodiagn. Untersuchungen über die Verwandtschaftsverh. innerhalb des Columniferen der Dikotylen. Bot. Archiv.
1913. HOLMGREN, I., Zur Entwicklungsgeschichte von *Butomus umbellatus*. Sv. Bot. Tidskr.
1916. —, Apogamie in der Gattung *Eupatorium*. Sv. Bot. Tidskr.
- 1880—82. HOOKER, J. D., Icones plantarum, 14.
1921. HÅKANSSON, A., Beiträge zur Entwicklungsgeschichte der Taccaceen. Bot. Not.
1923. —, Studien über die Entwicklungsgeschichte der Umbelliferen. Lunds Univ. Årskr. N. F., avd. 2. Bd. 18.
1901. JADIN, F., Contribution a l'étude des Simarubacées. Ann. sci. nat. bot., XIII.
1914. JACOBSSON-STIASNY, E., Versuch einer phylogenetischen Verwertung der Endosperm- und Haustorialbildung bei der Angiospermen. Sitzb. Akad. Wiss. Wien, math.-nat. Kl., 125.
1918. —, Zur Embryologie der *Aristolochiaceae*. Denschr. Akad. Wiss. Wien, math.-nat. Kl., 95.
1900. JUEL, H. O., Vergleichende Untersuchungen über typische und partenogenetische Fortpflanzung bei der Gattung *Antennaria*. Kgl. Sv. Vet. Ak. Handl., 33.

1907. JUEL, H. O., Studien über die Entwicklungsgeschichte von *Saxifraga granulata*. Nov. Act. Soc. Ups., IV.
1880. JÖNSSON, B., Om embryosäckens utveckling hos Angiospermerna. Lunds Univ. Årsskr., 16.
1891. KARSTEN, G., Über die Mangrove-Vegetation im Malayischen Archipelago. Bibl. Bot. Cassel.
1896. KERNER VON MARILAUN, A., Pflanzenleben I.
1896. KING, G., Materials for a flora of the Malyian Peninsula. Order XXVII *Meliaceae*. Journ. Asiat. Soc. Bengal., vol. 64.
1904. KIRCHNER, O., Partenogenesis bei Blütenpflanzen. Ber. d. d. bot. Ges., 22.
1859. KLOTZSCH, FR., Linnés nat. Pflanzenklasse Tricoccae. Berlin.
1896. KOEHNE, E., Zur Kenntnis der Gattung *Buxus*. Mitteil. der deutsch. dend. Ges.
1909. LAGERBERG, T., Studien über die Entwicklungsgeschichte und systematische Stellung von *Adoxa moschatellina* L. Kgl. Sv. Vet. Ak. Handl. Bd. 44.
1927. LANGLET, O., Über die Entwicklung des Eiapparates im Embryosack der Angiospermen. Sv. Bot. Tidskr., 21.
1902. LONGO, B., Osservazione sulle *Calycanthaceae*. Ann. ist. bot. di Roma.
1908. —, La poliembryonia nello *Xanthoxylon Bungei* Planch, senza fec. Bull. d. soc. bot. ital.
1868. MARCHAND, N. L. Recherches sur l'organisation des Burseracées. Paris.
1933. MAURITZON, J., Studien über die Embryologie der Familien *Crassulaceae* und *Saxifragaceae*. Akad. Abh. Lund.
- 1934a. —, Ein Beitrag zur Embryologie der Phytolaccaceen und Cactaceen. Bot. Not.
- 1934b. —, Zur Embryologie einiger *Gruinales*. Sv. Bot. Tidskr.
1925. MEYER, K. J., Parthenogenesis bei *Thismia javanica* im Lichte der Haberlandtschen Anschauung. Ber. d. d. bot. Ges., 43.
1909. MODILEWSKI, J., Zur Embryobildung von *Euphorbia procera*. Ber. d. d. bot. Ges., 27.
1910. —, Weitere Beiträge zur Embryobildung einiger Euphorbiaceen. Ibidem, 28.
1911. —, Über die Anomale Embryosackentwicklung bei *Euphorbia palustris* und anderen Euphorbiaceen. Ibidem, 29.
1907. MOTTIER, D. M., The development of the heterotypic Chromosomes in Pollen-Mother cells. Ann. of bot., 21.
1901. MURBECK, SV., Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Lunds Univ. Årsskr. Bd. 36.
1902. —, Über Anomalien des Nucellus und des Embryosackes bei parthenogenetischen Arten der Gattung *Alchemilla*. Ibidem, Bd. 38.
1869. MÜLLER, J., *Buxaceae*, in DE CANDOLLE: Prodromus. Pars. XVI, 1.
1926. NETOLITZKY, F., Anatomie der Angiospermen-Samen. LINSBAUER: Handb. d. Pfl. anat. X.
1844. NUTTALL, TH., On *Simmondsia*, a new Genus of Plants from California. Lond. Journ. of bot., 3.
1923. ORR, M. Y., Polyembryony in *Sarcococca ruscifolia* Stapf. Notes from the Roy. Bot. Gard. Edinburgh, 14.
1912. OSAWA, J., Cytological and experimental studies in *Citrus*. Journ. of agric., Vol. IV, 2. Tokyo.
1913. —, On the development of the Pollen grain and embryo sac of *Daphne*. Ibidem. Vol. IV, 5.
1904. OSTENFELD, C. H., Zur Kenntnis der Apogamie in der Gattung *Hieracium*. Ber. d. d. bot. Ges., 22.
1904. —, Weitere Beiträge zur Kenntnis der Fruchtentwicklung bei der Gattung *Hieracium*. Ibidem.
1904. OVERTON, J. B., Über Parthenogenesis bei *Thalictrum purpurascens*. Ibidem.
1914. PALM, BJ., Über die Embryosackentwicklung einiger Kompositen. Sv. Bot. Tidskr., 8.
1915. —, Studien über Konstruktionstypen und Entwicklungswege des Embryosackes der Angiospermen. Diss. Stockholm.
1922. —, Das Endosperm von *Hypericum*. Sv. Bot. Tidskr., 16.

1896. PAX, F., *Buraceae*, in ENGLER-PRANTL: Nat. Pflanz.-fam., III, 5.
1857. PAYER, J. B., *Traité d'organogénie comparée de la fleur*. Paris.
1846. PLANCHON, J. E., *Revue de la Famille de Simaroubées*. Hook. Lond. Journ. of Bot., 5.
1927. ROCÉN, TH., *Zur Embryologie der Centrospermen*. Diss. Uppsala.
1905. ROSENBERG, O., *Zur Kenntnis der Reduktionsteilung im Pflanzen*. Bot. Not., Lund.
1909. —, *Zur Kenntnis von den Tetradenteilungen der Compositen*. Sv. Bot. Tidskr., 3.
» —, *Cytologische und Morphologische Studien an *Drosera longifolia* × *rotundifolia**. Kgl. Sv. Vet. Ak. Handl. Bd. 43.
1917. —, *Die Reduktionsteilung und ihre Degeneration in *Hieracium**. Sv. Bot. Tidskr., 11.
- 1926—27. —, *Die semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen*. Hereditas, 8.
1913. SAMUELSSON, G., *Studien über die Entwicklungsgeschichte der Blüten einiger *Bicornes*-Typen*. Sv. Bot. Tidskr., 7.
1914. SCHMID, B., *Handbuch der naturgeschichtlichen Technik*. Leipzig u. Berlin.
- 1927—29. SCHNARF, K., *Embryologie der Angiospermen*. Berlin.
1931. —, *Vergleichende Embryologie der Angiospermen*. Berlin.
1920. SCHOCH, M., *Entwicklungsgeschichtlich-cytologische Untersuchungen über die Pollenbildung und Bestäubung bei einigen *Burmanna*-Arten*. Arb. Inst. Bot. u. Pflanzenphys. Univ. Zürich, 24.
1924. SCHÜRHOFF, P. N., *Zytologische Untersuchungen in der Reihe der *Geraniales**. Jahrb. wiss. Bot., 63.
1926. —, *Die Zytologie der Blütenpflanzen*. Stuttgart.
1919. SOUÈGES, R., *Les premières divisions de l'oeuf et les différenciations du suspenseur chez le *Capsella bursa pastoris* Moench*. Ann. sci. nat., 10 sér., bot.
1925. STENAR, H., *Embryologische Studien I u. II*. Akad. Abh., Uppsala.
1928. —, *Zur Embryologie der *Veratrum*- und *Anthericum*-Gruppen*. Bot. Not.
1921. STOLT, K. A. H., *Zur Embryologie der Gentianaceen und Menyanthaceen*. Kgl. Sv. Vet. Ak. Handl. Bd. 61.
1927. —, *Über die Embryologie von *Gentiana prostrata* Hänk. und die Antipoden der Gentianaceen*. Bot. Not.
1877. STRASBURGER, E., *Über Befruchtung und Zelltheilung*. Jena.
1878. —, *Über Polyembryonie*. Jen. Zeitschr. f. Naturw., 12.
1880. —, *Zellbildung und Zelltheilung*. Jena.
1905. —, *Die Apogamie der Eualchemillen und allg. Gesichtspunkte, die sich aus ihr ergeben*. Jahrb. f. wiss. Bot., 41.
1910. —, JOST, L., SCHENK, H., KARSTEN, G., *Lehrbuch der Botanik*. 10. Aufl. Jena.
1925. SVENSSON, H. G., *Zur Embryologie der Hydrophyllaceen, Borraginaceen und Heliotropiaceen*. Diss. Uppsala.
1926. —, *Zytologische und embryologische Solanaceenstudien. I. Über die Samenentwicklung von *Hyoscyamus niger* L.* Sv. Bot. Tidskr., 20.
1871. TIEGHEM, PH. VAN, *Recherches sur la structure du pistil et sur l'anatomie comparée de la fleur*. Paris.
1897. —, *Sur les Buxacées*. Ann. sci. nat., bot., sér. VIII, 5.
1905. —, *Sur les Irvingiacées*. Ibidem, sér. IX.
- 1921—22. TISCHLER, G., *Allgemeine Pflanzenkaryologie*. LINSBAUER: Handb. d. Pfl.-anat. Berlin.
- 1912—13. —, *Über die Entwicklung der Samenanlagen in parthenocarpen Angiospermen-Früchten*. Jahrb. wiss. Bot., 52.
1895. TRETJAKOW, S., *Die Beteiligung der Antipoden in Fällen der Polyembryonie bei *Allium odorum* L.* Ber. d. d. bot. Ges., 13.
1914. TÄCKHOLM, G., *Zur Kenntnis der Embryosackentwicklung von *Lopezia coronata* Andr.* Sv. Bot. Tidskr., 8.
1915. —, *Beobachtungen über die Samenentwicklung einiger Onagraceen*. Ibid., 9.

1922. TÄCKHOLM, G., Zytologische Studien über die Gattung *Rosa*. Acta Horti Berg., 7.
1878. WARMING, E., De l'Ovule. Ann. sci. nat., sér. 6.
1924. WETTSTEIN, R. von., Handbuch der systematischen Botanik. 3. Aufl., Leipzig u. Wien.
1930. WIGER, J., Ein neuer Fall von autonomer Nucellarpolyembryonie. Bot. Not.
1904. WINKLER, H., Über Parthenogenesis bei *Wikströmia indica* (L.) C. A. Mey. Ber. d. d. bot. Ges., 22.
1908. —, Über Parthenogenesis und Apogamie im Pflanzenreich. Progr. rei bot., 2.
1916. —, Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. Zeitschr. f. Bot., 8.
1914. WOODCOCK, E. F., Observations on the development and germination of the seed in certain *Polygonaceae*. Am. Journ. of Bot., 1.
1926. YAMAHA, G., Über die Zytokinese bei der Pollentetradenbildung, zugleich weitere Beiträge zur Kenntnis der Zytokinese im Pflanzenreich. Jap. Journ. of Bot., III.



Contents.

	Page
Preface	3
<i>Buxaceae</i>	5
Gynaeceum. Placentation	6
Archosporium. Integuments	9
The tetrad division.....	13
The development of the embryo sac.....	18
The fertilization	21
The endosperm	24
The embryo. Parthenocarp in <i>Buxus</i>	28
The nucellar embryony in <i>Sarcococca</i>	30
The seed	33
Abnormal ovules in <i>Pachysandra terminalis</i>	34
The pollen development	35
A word on the place of <i>Simmondsia</i> in the system.....	38
<i>Meliaceae</i>	40
Gynaeceum. Genesis, number and orientation of the ovules	41
Nucellus. Archosporium. Integument.....	45
The tetrad division. The formation of the embryo sac.....	54
Fertilization. Endosperm. Embryo	62
The seed testa	68
The pollen development	68
<i>Simarubaceae</i>	72
Gynaeceum. Genesis, number and orientation of the ovules	75
Nucellus. Archosporium. Integument.....	79
The tetrad division. Formation of the embryo sac.....	87
Fertilization. Endosperm. Embryo	95
The seed	103
Pollen development	103
<i>Burseraceae</i>	106
Gynaeceum. Genesis number, and orientation of the ovules	107
Nucellus. Archosporium. Integument.....	109
Tetrad division. Formation of the embryo sac	115
The development after fecundation	121
Pollen development	122
Bibliography	125

Pris 6 kr.